Historic, archived document

Do not assume content reflects current scientific knowledge, policies, or practices.

4B 137

UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1453

Washington, D. C. ▼ January, 1927

THE CHEESE SKIPPER AS A PEST IN CURED MEATS

By

PEREZ SIMMONS, Associate Entomologist, Stored-Product Insect Investigations
Bureau of Entomology

CONTENTS

	Page
Introduction	1
Systematic Position and Synonymy	2
Common Names	3
Distribution	4
Materials Infested	4
The Cheese Skipper and Disease	7
Nature of Injury to Cured Meats	8
The Adult Insect	9
The Egg	22
The Larva	22
Metamorphosis	28
Emergence of Adult	30
Life Cycle	30
Insects Found Associated with the Cheese Skipper	34
Control Measures	35
Summary and Conclusions	49
Literature Cited	51

WASHINGTON
GOVERNMENT PRINTING OFFICE
1927

UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1453

Washington, D. C. ▼ January, 1927

THE CHEESE SKIPPER AS A PEST IN CURED MEATS[1]

By PEREZ SIMMONS, *Associate Entomologist, Stored-Product Insect Investigations, Bureau of Entomology*

CONTENTS

	Page		Page
Introduction	1	The larva	22
Systematic position and synonymy	2	Metamorphosis	28
Common names	3	Emergence of adult	30
Distribution	4	Life cycle	30
Materials infested	4	Insects found associated with the cheese skipper	34
The cheese skipper and disease	7	Control measures	35
Nature of injury to cured meats	8	Summary and conclusions	49
The adult insect	9	Literature cited	51
The egg	22		

INTRODUCTION

These cheese skipper, *Piophila casei* (L.), has been mentioned in literature as a domestic pest since the middle of the sixteenth century and is one of the longest-known economic insects. A reference to this species can be recognized in the writings of Olaus Magnus (*46, p. 812*),[2] in 1567—a "kind of grub which infests cheese, leaping in the shape of a bow in fat cheese, and which no cold destroys" ("Vermis deniq; alius caseorum, salins instar arcus in pinguibus caseis, qui nullo frigore interimitur"). It is thus very certain that it was established in Europe before commerce with the Western Hemisphere had become extensive, and it seems improbable that the insect was introduced into Europe from the New World. Other pre-Linnean writers who were familiar with the cheese skipper include Redi (*58*), Goedaert (*27*), Frisch (*25*), and Merian (*50*). Redi's account is of especial interest because he used experiments with this fly to strengthen the evidence opposing the theory of spontaneous generation.

For a half century after Linné (*41 p. 597*) described it, in 1758, the cheese skipper was referred to in literature as a pest of cheese

[1] This bulletin represents a portion of the results of an investigation of the insect enemies of cured meats. The writer gratefully acknowledges the assistance of George W. Ellington, junior entomologist, who aided materially in obtaining much of the information in this report.

[2] Reference is made by number in italics to "Literature cited," p. 51.

but of no other stored food product. The fondness of the larvæ for ham was originally noted in the English edition of Systema Naturæ (*43, p. 610*) in 1806, and the first detailed account of injury to cured meats was given in France by Dufour (*19*) in 1844. In 1918 (*67*) it received considerable official attention in Europe, this time as a pest of brine-cured fish in Astrachan, on the Caspian Sea, where very serious damage was done for several years through various causes incident to the war.

The record of the cheese skipper in the United States curiously parallels its European history, but the first mention of injury to hams appeared many years later. In 1841 Harris (*30, p. 417*), who seems to have been the first outside of Europe to write of the insect, made no mention of infestation of cured meats. In 1870 Riley (*59*) gave cheese as the sole material in which oviposition took place; but in 1874 (*61, p. 100*) he reported that hams had been injured at St. Louis, in 1871, by "certain blowflies" which, he stated later (*62*), included flies which were identical with the adults of the cheese skipper. In 1880 (*62*) Riley reported further injury to meat products, one firm at Peoria, Ill., having lost over $2,000 worth of smoked hams from this pest. Serious injury at Kansas City in 1891 was reported by Kellogg (*37, pp. 114–115*); in a week as much as $1,500 worth of spoiled hams and bacon were returned by consignees.

In 1870 Willard (*80*) reported that "Immense losses are sustained every year on account of skippery cheese. Sometimes thousands of pounds * * * are tainted in this way * * *." According to Murtfeldt (*53, p. 171*), however, the situation had changed by the year 1893, when she asserted that the insect had within recent years become a far more serious pest of meats than of cheese, causing thousands of dollars' annual property loss and in addition "other thousands in labor and mechanical contrivances to keep it in check."

At the present time there are no indications that the American cheese industry suffers severe losses from the skipper, although this insect is still the principal cheese pest. Extensive losses occur, however, both to the meat trade and to farmers who cure small quantities of meat for home use. According to Howard (*35, p. 5*), Federal meat inspectors annually condemn over $1,000,000 worth of meat of all kinds on account of injury by insects, of which the skipper "is probably the most serious."

Piophila casei is without question the principal insect species attacking cured meats in the United States, and the value of meat actually destroyed in commerce, on farms, and at small abattoirs where there is no official inspection, plus the prorated cost of such preventive measures as screening and wrapping, added to injury to commercial reputations and loss of good will, undoubtedly make a total of large proportions.

SYSTEMATIC POSITION AND SYNONYMY

Piophila casei (Linné), type species of the genus Piophila of Fallén and dominant economic member of the acalyptrate muscoid family Piophilidae, was described in 1758 (*41, p. 597*) as *Musca putris casei.*

In 1775 Fabricius (*21, p. 780*) referred the species to the genus Musca, later, in 1805 (*22, p. 323*), assigning it to the genus Tephritis, in both instances under the specific name *putris*. The genus Piophila was erected on this species by Fallén in 1820 (*23*), but in 1822 Kirby and Spence (*39, p. 229*) referred it to the genus Tyrophaga; Curtis (*16, p. 126*) used the same nomenclature four years later. In 1855 Schiner (*68*) reviewed the synonymy of the species and concluded that *Piophila casei* Fallén (*23, p. 9*), *P. atrata* Meigen (*48, p. 396*), and *P. petasionis* Dufour (*19*) were one and the same. Rondani (*65, p. 249*), in 1874, stated that the *casei* of Linné (*41*), Fallén (*23, p. 9*), Meigen (*48, p. 395*), Macquart (*45, p. 541*), Zetterstedt (*83, p. 2510; 82, p. 772*), etc., was the same insect as the *atrata* of Fabricius (*22*), Meigen (*48, p. 396*), Macquart (*45, p. 542*), and Zetterstedt (*83, p. 2511; 82, p. 772*); the *vulgaris* (in part) of Fallén (*23, p. 9*); the *petasionis* of Dufour (*19*), and the *putris* (in part) of Linné (*41*) and Scopoli (*69, p. 337*). The species *affinis*, treated by Zetterstedt (*83*), and *melanocera*, referred to by Rondani (*65*), are questionably synonymous in the opinion of Melander and Spuler (*49, pp. 69–70*), recent reviewers of the sepsid and piophilid flies. These writers listed and described 17 species of Piophila from North America, and erected the family Piophilidae.

The generic name has been misspelled in literature as follows: By Riley (*60*) in 1870 as Peophila, by Mégnin (*47, p. 47*) as Pyophila; and again by Riley (*63, p. 226*) as Piophilus. Much of the confusion in the nomenclature seems to have been due to the variation in size of larvæ and adults, to the variety of food materials, and to certain color variations.

COMMON NAMES

The earliest writers used the term "cheese worm," "cheese maggot," or "cheese mite," the context, in the case of the last, leaving no doubt as to the pest designated. Swammerdam, in his extensive treatise on this insect (*73, pp. 63–75*), used the title "Acarus or mite," at the same time explaining that the true mite of cheese is an entirely different pest. Unless accompanied by some descriptive matter, early references to "mites" of cheese in nonscientific literature may refer either to the cheese skipper or to the acarids which infest cheese.

The following list includes the common names which appear in the literature of *P. casei*, the first being that recommended for exclusive use by the American Association of Economic Entomologists (*6, p. 524*):

cheese skipper
cheese-skipper
cheese mite
cheese-fly
cheese-maggot
cheese skipper fly
cheese and meat skipper
cheese-maggot fly
cheese and bacon hopper
cheese worm
cheese feeding fly
cheese and bacon fly
ham skipper
ham fly
ham worm
meat skipper
skipper-fly
skipper
jumper
hopper
hopper maggot
mite-fly
bacon and cheese hopper-fly

DISTRIBUTION

In common with many other domestic species, the cheese skipper has become widely distributed through commerce. There are records of its occurrence in nearly all countries of continental Europe, in England, India, the West Indies, Greenland, Alaska, and many localities in this country. In its capacity as a scavenger it is capable of perpetuating itself in carrion, and this is an excellent reason for believing that it has become established in many other parts of the world.

The records of cheese-skipper damage in the files of the Federal Bureau of Entomology include the District of Columbia and localities in the following States: Alabama, California, Illinois, Maryland, Massachusetts, New York, North Carolina, Pennsylvania, Tennessee, and Virginia. Melander and Spuler have specimens from Idaho, Kansas, Louisana, South Dakota, Texas, and Washington.

MATERIALS INFESTED

It was generally believed that the older, softer, and richer cheeses were most subject to attack, the accuracy of which opinion is evident from laboratory experiments in which the infestation of old dry cheese was observed to be a slow process. In the time of Redi (1688) (*58*) the epicures boasted that they knew how to grow worms in cheese to please the palate. Swammerdam (*73, p. 63*) stated that the worms were "generally held in detestation, though some eat them voluptuously with the rest of the cheese, from a vulgar notion, that they are formed out of the best parts of it * * *." Linné (*42, p. 456*) gave the habitat of this species as cheese; Scopoli (*69*) defined its food as soft, buttery, moist cheese; whereas Fabricius (*21, p. 780*) listed "dunghills, cheese and other fats."

The first mention of attacks on ham and bacon appeared, as already noted, in 1806. Bouché (*13, p. 99*) stated that the larvæ are found in human excrement, in the summer and fall; rotten fungus was given as a host food by Zetterstedt (*83, p. 2510*). John Curtis (*16, p. 126*) received larvæ from powdered rhubarb, and Germar (*26*) was given a sample of cooking salt infested with the larvæ, both occurrences probably being explainable by larval migration to these substances for pupation.

The occurrence of cheese-skipper larvæ in human cadavers was first recorded by Rondani (*65, p. 249*) in 1874. Large numbers of the larvæ were found infesting an exposed human cadaver at Paris in December, 1888, the account of which forms a part of Mégnin's treatise (*47, p. 170*) on the significance of the insect fauna of corpses in determining the date of death. The point in the entomological sequence in such cases chosen by Piophila, he stated, is that at which decomposition has reached the stage where fatty acids and caseous products are present, or from the third to the sixth month.

The findings of Mégnin were criticized and compared with their own observations by Johnston and Villeneuve (*36*). These investigators reported the examination of exposed cadavers in Canada, one in May and one in August, infested with the cheese skipper, which, they concluded, appears only after the saponification of the fat is well marked.

The only considerable work on the occurrence of this pest in human graves was done by Motter (*52*), at Washington, D. C., and reported in 1898. Doctor Motter found remains of this insect in at least 10 of the 150 graves examined, these 10 graves being from 3 to 10 years old and from 3 to 6 feet deep. These data not only invite speculation as to the avenue of invasion of graves by the species, but oppose the theory advanced by some writers that darkness is a condition repellent to the insect.

Murtfeldt (*53, p. 174*) was unable to obtain oviposition on fresh meat of any kind and she found that *P. casei* did not seem to be able to develop on salted but unsmoked meat. She reported that smoked beef is also attacked but not so severely as smoked pork. In the discussion following the reading of her article before the American Association of Economic Entomologists it was brought out that in England and continental Europe the custom exists " of placing cheese under the tap of a beer keg so that the drip would encourage the development of the insect."

Ormerod (*54, p. 9*) included salted beef in the list of food media of the cheese skipper, and stated that there is no doubt about the failure of the insect to oviposit in fresh meat.

According to the investigations of Howard (*33 p. 589*) the adult is attracted to human excreta.

Krausse (*40*) reported that sheep-milk cheese, an extremely salty product, swarmed with the maggots during the summer on the island of Sardinia.

A single record, not duplicated since, of infested oleomargarine was noted by Banks (*10, p. 35*).

Mote (*51, pp. 314–315*) found that both lean and fat beefsteak having a slightly putrid odor was apparently the most attractive food material to adults, exceeding in this respect lean and fat ham, lean and fat bacon, and Schweitzer cheese. He observed that " the adult flies lived longer, and the larvæ fed and matured more readily, on the beefsteak than on the other substances."

In his popular account of the cheese skipper, published in Italy, Berlese (*11, pp. 118–121*) made no mention of other food media than cheese.

Among the packing houses of the Middle West, Bishopp (*12, p. 271*) found skippers plentiful, especially among inedible materials in storage. Hoofs, horns, and particularly dried bones produced the insect in large numbers. Further observations under the same conditions were recorded by Laake in Pierce's work on Sanitary Entomology (*57, p. 455*). This investigator found skippers, often accompanied by hide beetles, swarming by millions in bone-storage houses. Improperly dried stocks of bones and hog hair are often infested with skippers and the larvæ of blowflies.

Bachmann (*9*) could not get the larvæ to thrive in fat ham or in bacon. After feeding on cheese, and in one case after feeding first on ham and then on cheese, larvæ were given common salt for a time, after which, he reported, pupation occurred. He also recorded having seen the larvæ living in water glass (sodium silicate).

The most extensive and graphic account of damage by the cheese skipper is that of Sakharov (*67*), a translation of whose interesting publication on the insect pests of cured fish in Astrachan has been

obtained. Although dealing with conditions not found in the United States, the following paragraph, an abstract of pertinent parts of his report, is of interest because it emphasizes the power of increase and destruction inherent in the cheese skipper in the presence of an unlimited food supply resulting from careless sanitation:

> Very large quantities of fish are smoked at the Astrachan fisheries, but on account of the ability of the cheese skipper to infest this product the smoking is discontinued in summer. Fish packed in barrels and covered with brine has been very severely attacked by the insect, which is the chief pest and the only dipterous enemy of fish preserved in this way. Because of the use, during the Great War, of imperfectly seasoned lumber to make the barrels, cracks appeared in the latter as they dried, allowing the brine to leak out. The eggs of *P. casei* were laid in the moist cracks thus formed and the young larvæ entered the barrels, often reducing the contents to a formless mass of flesh and skeletons. On account of the war, also, the ice supply in the storage houses was below normal and this condition promoted increase of the pest. At one plant the puparia among and under the barrels of fish could be gathered by the shovelful; in another ice house the floor was so covered with puparia that it resembled the floor of a grain elevator.

Sakharov also stated that the insect attacks green sealskins.

A list of the food materials of the larvæ and adults which are reported in the literature of *Piophila casei* includes cheese, bacon, ham, human excrement, rotten fungus, human corpses (both buried and exposed), oleomargarine, smoked beef (also known as dried beef or beef hams), putrid beefsteak, salted beef, hoofs, horns, dried bones, moist hog hair, smoked fish, fish in brine, and green sealskins. Verbal reports to the writer state that infestations have been known to occur in marrow bones and in lard. Common salt and water glass are recorded as larval foods, but these records are open to question. It should be noted, also, that flies of other species of Piophila (immature forms unknown), closely resembling *P. casei*, occur out of doors; consequently some recorded observations may have been incorrectly assumed to relate to the cheese skipper. Furthermore, larvæ of certain flies of the families Ortalidae and Drosophilidae and of the genus Lonchaea also possess the ability to skip, according to C. T. Greene, of the Bureau of Entomology.

The writer has not succeeded in rearing skippers in the circummuscular fat of ham, and in general it appears that the generic name Piophila (derived from the Greek πιον, fat, and φιλος, loving) is not strictly appropriate. The fat parts of cured ham are not nearly so attractive for oviposition or feeding purposes as are the lean portions and the connective tissue—points which will receive further attention in this discussion. Both smoked herring and salted herring supported the life cycle in the laboratory. Semiliquid putrid beef, Bologna sausage, several varieties of cheese, the marrow of ham bones, and lean ham have proved suitable media. An attempt to rear the insect on decomposing mushrooms was unsuccessful, no progress was made by larvæ in lard substitute, and a number of trials with ham fat showed that it was entirely unfavorable as a food, although this may have been due partly to suffocation of the larvæ by the melted fat.

A flask containing several thousand puparia, many of them in a fermenting condition because of metabolic moisture confined in the stoppered container, was observed to be infested with the mag-

gots of the skipper, some adults having been able to emerge and produce eggs. A number of the larvæ were able to pupate under these adverse conditions. The attribute of resistance of the cheese skipper to unfavorable conditions is referred to on succeeding pages. Infestations in bacon, salt pork (unsmoked), and dried cooked bones have been observed by the writer.

By far the greatest damage to edible products in this country is done to hams and shoulders which have been cured and smoked. In the writer's experience the fresher these are the more rapid the progress of the infestation. Old pieces of meat which have become hard and dry, sometimes covered by a coating of blue mold and by a salvelike layer of fat, seem to be relatively immune from attack.

THE CHEESE SKIPPER AND DISEASE

Were it not for the fact that stored food products such as ham and bacon are usually cooked before being eaten, the possibilities for the adult fly to bring infection to human beings through the medium of polluted food might be considerable. The sources from which the flies may come include some which are extremely filthy. Aside from differences in size and abundance, adults of *P. casei* might be viewed with much the same concern as are now those of the house fly (*Musca domestica* L.). Visits of the adults to cheese, which is usually eaten uncooked, might result in the spread of enteric diseases and other maladies. Although no experimental evidence is at hand to indict this species, its haunts and habits do not absolve it from suspicion as a possible vector of disease.

The custom of consuming infested cheese has sometimes caused much discomfort to those who have indulged themselves in it. Thébault (*76*) concluded that larvæ can pass through the intestines of man without dying, and that serious intestinal lesions are caused by them. Similar conclusions have been reached by Alessandrini (*4*, *5*), and this investigator found that the same is true of dogs, in which intestinal lesions are always caused when they are fed with the maggots. Austen (*8*, *pp. 13–14*), Banks (*10*, *p. 35*), Pavloski (*56*), and Colombe and Foulkes (*14*) also reported cases of intestinal myiasis. This is the insect most often found in the intestines of man, according to the publication of the Office of the Secretary of Agriculture on the insects of military camps (*77*, *p. 8*). It has even been known to pupate in the human intestine and there to develop into adults, causing intense colic (*71*). The case of a woman who suffered from larvæ of *P. casei* in the nose was reported by Bond (*2*). Austen (*8*) stated that in Italy the larvæ "have been expectorated by a patient suffering from an infection of the chest." According to Riley and Johannsen (*64*, *pp. 137–138*), Portschinsky found several dead larvæ of this species in the appendix of a dog.

From the foregoing compilation of cases it is evident that to swallow the larvæ of this insect, equipped as it is with sharp oral hooks or claws, and with extraordinary powers of resistance, may result in much discomfort. The utter inconsistency of people who eat these maggots has been pointed out by Berlese (*11*, *pp. 118–121*), who argued that those who prefer skippered cheeses would turn in disgust from food polluted by an adult fly of the same species.

NATURE OF INJURY TO CURED MEATS

The injury to cured meats which results from cheese-skipper infestation is usually deep-seated. This is in contrast to the work of other ham pests such as the red-legged ham beetle (*Necrobia rufipes* DeGeer), which usually burrows near the surface in the soft fat or just beneath the hide, and the larder beetle (*Dermestes lardarius* L.), which is also typically a surface feeder. The favorite starting place for skipper infestation is at the butt end of newly smoked hams and shoulders. Here, where the soft muscles and the connective tissue are exposed in cross section, are ideal feeding areas, the muscles often being somewhat separated, a condition which encourages penetration by the maggots. In hams entrance is effected frequently

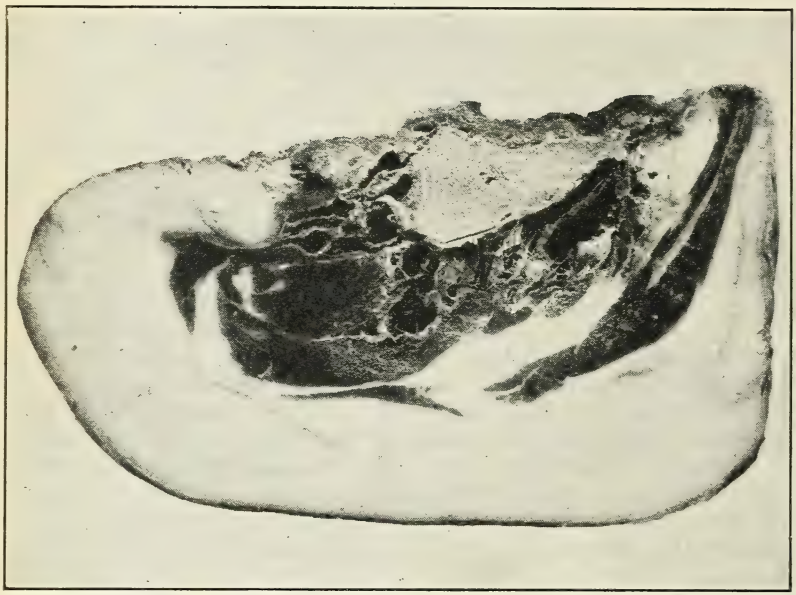

FIG. 1.—Cross section through middle of a dry-cured ham badly injured by feeding of larvæ of *Piophila casei*. The outer layer of fat at the upper left has collapsed over the eaten-out cavities. Much reduced

around the exposed bone on the inside, and less often at the hock end where the string passes through, in the small but deep holes left by the inspector's trier, and in small cuts. In the usual well-advanced infestation the insects are found at the center of the meat, in the vicinity of the joint of the bones.

In cured meat, putridity does not usually become marked until the infestation is rather old and consequently fouled by larval excreta. New colonies of the larvæ, even though extensive, have little offensive odor, but the cavities of hams infested for some time give off a strong moldy-sour odor similar to that of old brood comb.

Murtfeldt (*53, p. 172*) noted the lack of putrefaction in infested hams, but Sakharov (*67*) has given data to show that in infested fish the skipper maggots have a symbiotic relationship with an undetermined putrefactive organism.

FIG. A.—*Piophila casei:* Adult male. × 13
FIG. B.—*Piophila casei:* Adult female. × 13

An advanced case of cheese skipper infestation in ham is shown in Figure 1. The history of this infestation is given herewith to bring out several points of interest, particularly the fact that large numbers of the insects may develop in one piece of meat.

This dry-cured ham weighed 21 pounds and 4 ounces when removed from the smoke on May 14, 1920. On August 15 it was found to be infested, discarded as inedible, wrapped in paper, and placed in a cotton sack. On May 10, 1921, after being stored during the winter in a cold building, there were found to be 14,819 puparia, nearly all empty, among the folds of the paper and on the surface of the meat. Apparently none of the adults were able to escape, but large numbers of dead ones were present. From May 13 until July 15, 1921, on which latter date the ham ceased to produce skippers, probably because of the presence of the predacious ham beetle *Necrobia rufipes*, 37,808 full-grown larvæ migrated from the interior of the meat, making the total recorded production of skippers 52,627. On October 31, 1921, this ham weighed 15 pounds, thus showing a loss in weight, due to evaporation, the feeding of the skippers, and (toward the end of the observations) to some feeding by ham beetles, of 6 pounds and 4 ounces in 18 months. The daily migration of mature larvæ from the ham is recorded in Table 1.

TABLE 1.—*Daily migration of larvæ of Piophila casei from an infested ham from May 13 to July 15, 1921, at Washington, D. C.*

Date	No.	Date	No.	Date	No.	Date	No.	Date	No.
May 13	75	May 27	308	June 10	648	June 24	988	July 8	266
14	64	28	342	11	754	25	1,150	9	254
15	152	29	333	12	758	26	920	10	171
16	310	30	610	13	1,173	27	989	11	97
17	417	31	799	14	1,265	28	887	12	66
18	303	June 1	772	15	1,250	29	731	13	38
19	280	2	813	16	1,230	30	667	14	38
20	249	3	879	17	1,226	July 1	591	15	30
21	337	4	753	18	992	2	546		
22	556	5	741	19	957	3	410		37,808
23	437	6	837	20	878	4	328	[1]+14,819	
24	763	7	721	21	949	5	340		
25	444	8	689	22	990	6	332	Total	52,627
26	266	9	606	23	769	7	274		

[1] Migrated before May 13.

THE ADULT INSECT

TECHNICAL DESCRIPTION

Head black above, the front sericeous except for the large ocellar triangle, toward the antennæ narrowly yellow; occiput finely roughened, polished, the lower occipital orbits narrowly pruinose; face, cheeks, mouth parts and antennæ yellow, the cheeks greatly broadened behind, vibrissæ prominent, oral hairs weak or absent; third joint of the antennæ short, oval, the arista brown. Notum black, with faint ænescent tinge, not smoothly polished but minutely roughened, bearing three rows of fine setulæ in lieu of the irregularly scattered hairs of the other species of Piophila; mesopluræ with scattered minute hairs, propluræ pollinose, the bristle evident; scutellum convex. Abdomen more oblong than usual, the black pubescence conspicuously long. Legs largely black and hairy, coxæ, trochanters, knees, and posterior tarsi more or less yellow. Wings hyaline, veins pale, anterior crossvein shorter than usual but variable, located beyond the middle of the widened discal cell, basal cells indefinitely wider than usual, anal vein evanescent some distance before the margin.

Length 2.5 to 4 mm.

The foregoing description has been taken from Melander and Spuler (*49, p. 69*).

GENERAL DESCRIPTION

The flies (Pl. 1, A, B),[3] as Redi (*58, p. 74*) described them, are "small flies resembling winged ants, which immediately after birth skipped about with incredible sprightliness and vivacity so that they seemed to be the embodiment of perpetual motion." Superficially this species appears shining black, with reddish-brown eyes,

FIG. 2.—Skipper flies and three specimens of the common house fly, showing comparative sizes. × 2

and wings held flat over the dorsum when at rest. The females are usually larger than the males, and the largest ones are about three-fifths as long as an average-sized house fly and more slender. The comparative sizes of skipper flies and house flies are shown in Figure 2. When feeding and courting the flies are feverishly active, run-

[3] Sibyl Swegman MacDonald, insect delineator with the Bureau of Entomology, prepared the drawings shown as Figures 2, 3, 8, and 9, and J. G. Pratt, scientific photographer of the bureau, made the photographs.

ning, making short jumping flights, cleaning themselves, and engaging in brief, vigorous sparring matches with other flies. In these bouts the forelegs are used the most and are employed to seize and shake the opponent. When not feeding, mating, or ovipositing the flies may be found at rest, usually on a vertical surface. They may be easily captured in a vial or killed with the hand.

The ovipositor of the female is a three-jointed telescopic organ, hyaline, with a black, slightly hairy, chitinized tactile tip. Some chitinous reinforcing lines are present, these lines on the proximal joint being sparsely hairy. The proximal joint of the extended ovipositor is twice as long as the other two combined, and the opening of the tube is between the second joint and the tip or distal joint. The abdomen of the female is pointed, that of the male blunt.

The external reproductive organs of the male consist of a basal knob bearing the copulatory claspers and a coiled filiform penis nearly equal in length to the entire insect and coiled out of sight beneath the right hand of the two dorsal asymmetrical scales which protect the terminal segment of the insect. The penis is reinforced with a hirsute black line of chitin, which chitinization, having a permanent tendency to coil, seems to be the means whereby the insect is enabled to return the organ to its serpentine position beneath the dorsal scale.

The mouth parts of the adult are similar in structure to those of the house fly, the distal end of the proboscis being provided with a perforated pad, of gridiron pattern, which functions as a strainer.

MATING

Before the newly emerged female has assumed the adult form and color, and often when she is but a soft transparent sac with wrinkled wing pads, she is beset by the male flies. The act of mating, which is consummated with great vigor, continues for a length of time which is controlled by the temperature. Several records are given to illustrate this: In a number of trials at 65° F. pairs remained in copula as follows: Two pairs 9½ minutes, 1 pair 10 minutes, 1 pair 11 minutes, 1 pair 19 minutes. At 75° F. 2 pairs remained in copula 5½ minutes and other pairs, respectively, 6, 6, and 8 minutes. At times, with room temperatures in the neighborhood of 90° F., the mating impulse was markedly decreased.

Mating takes place more than once in the case of pairs confined in vials. Ovipositing females are not molested by the males, and are sometimes observed in groups, apart from any males, depositing eggs in masses. The act of mating is terminated by vigorous efforts of the female, but in the case of old flies, with body fluids and strength depleted, the separation often can not be made and in the laboratory considerable numbers of confined flies die in copula. Of 1,353 flies which died when confined without water, 60 pairs and 3 trios (9.5 per cent) met death in this condition. Microscopic examination of the trios showed that in each case two males were actually in copula with a single female. It is not probable that death in copula often precedes oviposition, but the writer has observed its occurrence.

FEEDING OF THE ADULT

Suitable moist food is a prerequisite to normal oviposition. The adults lack the power to soften desiccated food, and because of the structure of the mouth parts can not do more than "lap" and suck semiliquid or liquid materials. Oviposition does not occur, or takes place infrequently, when the supply of proper food is insufficient. Flies given water alone do not lay eggs. Water is frequently sought by the adults, which were often found in the laboratory about dripping faucets.

Murtfeldt (*53*, *p. 174*), one of the few who have considered the matter of adult feeding, stated that "It will sip a little at sweets, * * * while the odor of smoked meats speedily summons it." She reported that the flies were first noticed in the packing houses around vats of yellow wash—a mixture of glue, rye flour, coloring matter, and water. Mote (*51*, *pp. 314–315*), as previously stated (p. 5), found that the adults live longer on putrid beefsteak than on ham, bacon, or cheese. Lodge (*44*, *p. 486–487*) stated that peptone, both moistened with water and mixed with bread, and sometimes containing maggots, attracted many adults of *P. casei*. She found a casein bait effective. Sakharov (*67*) reported that these flies can feed on many substances, even the nectar of flowers.

Although adults live without food for several days in warm weather, as shown elsewhere (Table 8), nourishment prolongs the life of both sexes, especially of the males. This appears to be due to the fact that fed females oviposit and the consequent drain upon their vitality results in earlier death. In one trial about 200 unfed and unwatered adults were given thin slices of juicy ham; this was immediately covered with the flies, lapping at the surface with rapid, shifting pecks, like chickens eating scattered grain. Water-soaked cotton was then introduced, but failed to lure more than a few flies from the meat. Fresh pieces of cheddar cheese were eagerly attacked by them, but once the surface of these foods became lapped dry no more nourishment could be obtained.

Water-soaked cotton attracted many flies when offered to a large number of them which were thirsty. Some were observed to draw drops of water away from the main supply and then to suck it up from the glass; others inserted their proboscides through the surface film of the main supply. In one experiment newly emerged adults which were fed upon fresh cheese, and were thereby enabled to reproduce, soon became unable to obtain food on account of the hardening of the cheese, but began feeding again a few days later, after their progeny, with ability to soften the cheese, had reduced it to a paste.

Bachmann (*9*) stated that the adults regurgitate droplets of liquid food, after the manner of house flies, but the writer has not been able to observe this.

The odor of putrid meat is attractive to cheese-skipper adults. Cultures of larvæ in putrid ham unfailingly attract most of the adults in the room, and the same is true of strong-smelling cheese, decaying beef, and freshly cured ham. Adults confined with semiliquid, putrid beef gorged themselves with it until they were noticeably distended, and oviposition was observed to be profuse.

PREOVIPOSITION PERIOD

At summer temperatures and in the presence of a moist food medium, the laying of fertile eggs usually begins in about 24 hours after newly-emerged adults have been mated. With less favorable conditions the preoviposition period is lengthened, the determining factors being temperature and food supply. Table 4 shows typical preoviposition periods. One female 24 hours old laid eggs 3 hours after mating, but these did not hatch. Fertile eggs have been secured 10½ hours after the mating of newly emerged flies.

OVIPOSITION

The process of egg laying is accomplished in a rapid manner, eggs being deposited every three or four seconds or at longer intervals. The female runs about over the meat in nervous haste with her ovipositor extended and its tip, held downward at an angle with the ovipositor, touching the surface. As she goes actively about she feels the surface with the tactile extremity of the ovipositor moving from side to side and exploring crevices in the meat. No sooner has an egg been deposited than another appears in the translucent basal segment of the ovipositor, whence it is rapidly ejected at the will of the fly. As the egg passes through the opening in the ovipositor the latter often bends sharply for an instant, whereupon the egg is wiped off by contact with the meat. The eggs are laid singly or in groups on the surface of the meat or, where many flies are present, are packed by thousands into crevices where the membranous connective tissue seems to fill the requirements of the females for an ideal location. The laying of eggs in masses favors the development of the progeny, as indicated later. In vials where the meat was placed on cardboard, eggs were often laid between the meat and paper, arranged in groups like the pleats of an open fan.

In the time of Redi (1688) the process of oviposition had evidently not been observed. Most people believed in the spontaneous generation of low forms of life, particularly those found in filth. An interesting theory, mentioned also by Redi (*58*, *p. 73*), was that of Gassendi, who believed that the skipper flies deposited their eggs on grass, which was eaten by cows, sheep, and goats and thereby introduced into milk and cheese.

A female fly in the act of thrusting her ovipositor through the meshes of a linen bag covering a ham was observed by Dufour (*19*).

The observations of Kellogg (*37*, *pp. 114–115*) in infested packing houses at Kansas City showed that the adults were literally swarming in the smoky sacking rooms where hams were being wrapped and in the smoke-filled shaft where the meats were smoked. The eggs were laid upon the hams even while the meat was in the wrappers' hands, with the result that the wrapped hams were infested before being shipped.

Murtfeldt (*53*, *p. 173*), however, found that the eggs were deposited on the wrapper, preferably among the folds or in spots where the fat had penetrated and loosened the yellow wash. Sakharov (*67*) asserted that eggs are not deposited on a dry medium, but the writer has observed eggs upon the dry muslin cover of a jar of strong-smelling cheese. It is evident that actual contact with the proposed

larval food is usually but not always necessary for the deposition of eggs. According to the writer's observations, eggs laid on a dry surface (that is, one that is neither damp nor greasy) do not hatch.

FECUNDITY

Swammerdam (*73, p. 74*) dissected an adult female and found that the ovaries contained 256 eggs. In 1861 Taylor (*75, p. 609*) reported that nearly 300 eggs were laid, but more recently published data show much smaller numbers. The average number of eggs laid by females in Murtfeldt's experiments (*53, p. 173*) was 30, and several dissections made by Sakharov (*67*) gave an average of 64 eggs, a maximum of 84, and a minimum of 44.

Sakharov computed the probable increase of the cheese skipper in Astrachan, basing his computations on an average of 60 eggs per female and assuming the resulting progeny equally divided as to sex. Starting with a pair of flies in April, he estimated that the total progeny of five generations (the minimum number during the Astrachan summer) amounted to 50,279,860.

With two generations a month at Washington during the summer, and at least double the average individual reproduction figures used by Sakharov, it is apparent that the cheese skipper is potentially extremely prolific in climates like that of the District of Columbia. The limited food list of this species, together with the care which is usually taken to guard edibles and dispose of carrion, prevents the enormous increase of which the species is capable.

Table 2 details some of the oviposition records made in 1921 on several foods at Washington, D. C.

TABLE 2.—*Oviposition records of Piophila casei on various food materials at Washington, D. C., in 1921*

Date emerged	Date mated	Day after mating and number of eggs laid							Longevity		Total eggs	Remarks
		1st	2d	3d	4th	5th	6th	7th	Male	Female		
									Days	*Days*		
June 1	June 1	87	0	91	----	----	----	----	3	4	178	On lean ham.
1	1	0	99	----	----	----	----	----	3	4	99	Do.
1	1	55	----	----	----	----	----	----	7	4	55	Do.
6	6	----	----	----	----	----	----	----	3	5	0	On dried beef.[1]
6	6	----	----	----	----	----	----	----	5	6	0	Do.
18	18	95	80	----	----	----	----	----	7	3	175	On lean ham.
18	18	43	----	----	----	----	----	----	4	2	43	Do.
18	18	85	1	----	----	----	----	----	6	2	86	Do.
18	18	78	87	5	11	22	----	----	6	5	203	Do.
18	18	93	0	66	----	----	----	----	7	4	159	Do.
28	28	30	31	----	----	----	----	----	3	3	61	Do.
28	28	128	----	----	----	----	----	----	6	4	128	Do.
28	28	68	61	----	----	----	----	----	3	2	129	Do.
July 7	July 7	----	----	----	----	----	----	----	3	2	0	On lean Smithfield ham.
7	7	----	----	----	----	----	----	----	8	3	0	Do.
7	7	----	----	----	----	----	----	----	4	2	0	On Smithfield ham fat.
8	8	----	----	----	----	----	----	----	5	2	0	Do.
8	8	----	----	----	----	----	----	----	5	2	0	Do.
13	13	65	----	----	----	----	----	----	7	6	65	On lean Smithfield ham.
13	13	----	----	----	----	----	----	----	8	2	0	Do.
13	13	85	----	----	----	----	----	----	14	7	85	Do.
13	13	----	----	----	----	----	----	----	7	3	0	Do.
13	13	----	----	----	----	----	----	----	8	3	0	Do.

[1] Dried beef and Smithfield ham are unsuitable as food for adults and larvæ because they contain comparatively little water.

TABLE 2.—*Oviposition records of Piophila casei on various food materials at Washington, D. C., in 1921*—Continued

Date emerged	Date mated	Day after mating and number of eggs laid							Longevity		Total eggs	Remarks
		1st	2d	3d	4th	5th	6th	7th	Male	Female		
									Days	*Days*		
July 19	July 20	58	51	0	22				8	8	131	On lean ham.
20	20	70	0	27	0	44	0	41	11	11	182	Do.
22	22	0	19						2	5	19	Do.
Sept. 1	Sept. 1	73	63						10	3	136	Do.
1	1	66	63						26	4	129	Do.
1	1	73	65	0	0	14			8	6	152	Do.
1	1	66	0	36					5	4	102	Do.
1	1	45	14						9	2	59	Do.
1	1	36	60						11	5	96	Do.
8	8	54	0	0	23				14	13	77	Do.
8	8	0	54	0	31				10	4	85	Do.
8	8	60	0	24					18	5	84	Do.
8	8	49							5	5	49	Do.
8	8	0	44						14	5	44	Do.
8	8	60	0	0	16				3	4	76	Do.
7	8	0	37	0	0	19			12	6	56	Do.
7	8	63							6	5	63	Do.
15	15	37	0	31					3	3	68	Do.
15	15	66	33						6	3	99	Do.
30	Oct. 1								39	31	0	On lean ham in refrigerator.
30	1	73	78						7	7	151	On lean ham.
30	1	101	83						17	7	184	Do.
30	1	0	85						13	9	85	Do.

Table 3 gives the daily mean temperatures in the laboratory during the time the records shown in Table 2 were being made.

TABLE 3.—*Daily mean temperatures in the laboratory at Washington, D. C., in 1921, during the period when the experiments on Piophila casei shown in Table 2 were made*

[Based on daily average of thermograph readings taken at two-hour intervals]

Date	Temperature	Date	Temperature	Date	Temperature	Date	Temperature	Date	Temperature
	°F.		°F.		°F.		°F.		°F.
May 19	74	June 24	89	July 30	82	Sept. 4	84	Oct. 10	69
20	74	25	89	31	85	5	82	11	75
21	76	26	89	Aug. 1	78	6	81	12	74
22	80	27	87	2	78	7	79	13	71
23	82	28	86	3	80	8	79	14	70
24	72	29	86	4	83	9	79	15	71
25	67	30	85	5	82	10	79	16	68
26	71	July 1	82	6	84	11	80	17	69
27	69	2	83	7	78	12	80	18	72
28	74	3	86	8	78	13	79	19	73
29	76	4	88	9	79	14	76	20	74
30	76	5	88	10	75	15	78	21	70
31	74	6	83	11	74	16	77	22	72
June 1	76	7	84	12	75	17	79	23	69
2	75	8	88	13	78	18	82	24	71
3	74	9	88	14	82	19	75	25	68
4	78	10	87	15	75	20	73	26	67
5	74	11	84	16	73	21	75	27	70
6	73	12	81	17	72	22	76	28	73
7	72	13	82	18	79	23	75	29	74
8	72	14	83	19	79	24	73	30	68
9	74	15	82	20	80	25	75	31	73
10	76	16	78	21	81	26	71	Nov. 1	73
11	80	17	80	22	74	27	69	2	70
12	82	18	80	23	73	28	74	3	69
13	84	19	83	24	73	29	78	4	69
14	82	20	84	25	73	30	76	5	68
15	78	21	81	26	72	Oct. 1	68	6	59
16	78	22	79	27	72	2	67	7	63
17	82	23	79	28	73	3	68	8	69
18	80	24	81	29	80	4	66	9	69
19	79	25	85	30	84	5	67	10	69
20	78	26	84	31	85	6	69	11	57
21	81	27	86	Sept. 1	85	7	70	12	64
22	85	28	86	2	85	8	73	13	56
23	88	29	83	3	85	9	61		

Further oviposition experiments, in which lean ham was used as food for adults and larvæ, are given in Table 4. The temperatures affecting them are given in Table 5.

TABLE 4.—*Oviposition of Piophila casei on lean ham at Washington, D. C., in 1922*

Date emerged	Date mated	Day after mating and number of eggs laid														Total eggs	Longevity of female
		1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th		
																	Days
Aug. 28	Aug. 28	0	52													52	5
28	28	0	65	66	75											206	6
28	28	0	111	0	2											113	6
28	28															0	2
28	28	0	97	56	0	19										172	6
28	28	0	106													106	5
28	28	0	130	0	0	5										135	5
28	28	0	140	0	93	0	89	0	37							359	9
28	28															0	2
28	28	0	0	0	45											45	5
29	29	40														40	3
29	29	75	63													138	3
29	29	0	145													145	5
29	29	0	78	0	27											105	5
29	29	67														67	7
29	29	0	13	51												64	5
29	29	0	10	72												82	3
29	29	0	45	67	21											133	7
29	29	0	70	62	0	0	20									152	7
29	29	0	32	79												111	5
30	30	82	46													128	5
30	30	70	72	0	48	0	0	0	0	26						216	12
30	30	79	87	0	6											172	7
30	30															0	1
30	30	38	35													73	3
31	31	55	0	72	82											209	6
31	31	81														81	3
31	31	39	22													61	4
31	31	0	50													50	4
31	31															0	2
Sept. 4	Sept. 4	0	86	25												111	3
4	4	52														52	4
4	4	70	38													108	5
4	4	54														54	3
4	4	0	30													30	4
4	4	0	80													80	3
4	4	110	0	31												141	4
4	4	27	87													114	3
27	27	0	63	70												133	6
27	27	0	75	0	0	0	66	0	0	117	0	29				287	12
27	27	0	147	0	0	0	0	0	73	96	0	52				368	12
27	27	0	57	0	109	0	0	0	0	0	43	0	29	42		280	17
27	27	0	97	0	95	0	0	0	0	40	73	0	0	52		357	18
27	27	0	87	0	89	0	0	0	74	60	4	61				375	17
27	27	0	89	0	0	0	0	0	89	0	55	0	0	0	44	277	19
27	27	0	89	0	73	0	0	0	0	90	92	83	53			480	12
27	27	0	88	21	5	0	0	8	0	0	65	13				200	11
27 [1]	27															0	10
27 [1]	27	0	0	110	0	0	27	0	4							141	11
27 [1]	27	0	0	0	0	0	72	0	56							128	9
27 [1]	27	0	151													151	3
27 [1]	27	90	101	0	73	0	24	0	38	28						354	9
27 [1]	27	0	159	78	0	0	43									280	6
27 [1]	27	0	117	0	0	0	31	127	0	73	77					425	12
27 [1]	27	0	0	0	0	0	87	36	48	0	0	30				201	12
Oct. 4	Oct. 4	81	63	0	53	0	0	12	0	47	0	0	0	12		268	16
4	4	70	86	0	0	0	0	57	0	0	0	0	0	0	60	273	22
4	4	92														92	6
4	4	16	62													78	5
4	4	79	63	31	48	0	0	0	61							282	10
4	4	74	72													146	6
4	4	54	83	0	49	0	0	39								225	12
4	4	0	79													79	2
4	4	39	89	0	0	86	0	47	0	0	0	0	0	72		333	17
4	4	89	58	0	55											202	13
4	4	74	71													145	6
4	4	49	72													121	6

[1] In incubator at 80 to 85° F.

TABLE 4.—*Oviposition of Piophila casei on lean ham at Washington, D. C., in 1922*—Continued

Date emerged	Date mated	Day after mating and number of eggs laid													Total eggs	Longevity of female
		1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th	
																Days
Oct. 15	Oct. 16	0	0	87	0	0	0	0	130	0	0	0	0	0	0	[2] 224	26
15	16	0	0	57	0	61	0	0	61	0	0	0	0	41	----	220	24
15	16	0	0	60	0	0	0	0	0	64	----	----	----	----	----	124	26
15	16	0	0	40	0	15	----	----	----	----	----	----	----	----	----	55	29
15	16	0	13	2	0	0	0	24	96	----	----	----	----	----	----	135	15
15	16	0	62	0	0	0	0	123	----	----	----	----	----	----	----	185	10
15	16	0	35	0	0	19	17	0	27	23	0	0	0	13	----	134	22
15	16	0	54	0	57	0	0	84	0	41	----	----	----	----	----	236	13
23	23	0	0	0	0	74	----	----	----	----	----	----	----	----	----	74	16
23	23	0	81	0	25	42	----	----	----	----	----	----	----	----	----	148	16
23	23	0	8	70	----	----	----	----	----	----	----	----	----	----	----	78	12
23	23	0	0	0	0	0	0	0	89	----	----	----	----	----	----	89	11
23	23	0	0	35	----	----	----	----	----	----	----	----	----	----	----	35	16
23	23	0	84	0	0	33	----	----	----	----	----	----	----	----	----	117	21
23	23	0	91	0	65	----	----	----	----	----	----	----	----	----	----	156	16
23	23	0	0	0	0	18	----	----	----	----	----	----	----	----	----	18	7
23	23	0	0	85	----	----	----	----	----	----	----	----	----	----	----	85	3
23	23	0	0	84	----	----	----	----	----	----	----	----	----	----	----	84	16
23	23	0	0	55	----	----	----	----	----	----	----	----	----	----	----	55	21
23	23	0	0	54	----	----	----	----	----	----	----	----	----	----	----	54	3
23	23	0	0	64	----	----	----	----	----	----	----	----	----	----	----	64	12
23	23	0	0	73	0	0	0	0	63	----	----	----	----	----	----	136	21
23	23	0	0	68	----	----	----	----	----	----	----	----	----	----	----	68	10
23	23	0	0	0	0	0	0	0	65	----	----	----	----	----	----	65	12
23 [1]	23	73	0	68	0	0	19	0	48	----	----	----	----	----	----	208	12
23 [1]	23	72	67	----	----	----	----	----	----	----	----	----	----	----	----	139	7
23 [1]	23	79	69	0	0	0	0	0	26	----	----	----	----	----	----	174	11
23 [1]	23	76	77	0	0	37	----	----	----	----	----	----	----	----	----	190	5
23 [1]	23	74	0	70	0	0	33	----	----	----	----	----	----	----	----	177	7
23 [1]	23	80	92	0	0	0	36	0	0	51	----	----	----	----	----	259	11
23 [1]	23	101	0	92	0	40	35	0	0	50	----	----	----	----	----	318	14
23 [1]	23	87	70	----	----	----	----	----	----	----	----	----	----	----	----	157	2
23 [1]	23	67	56	0	0	0	0	0	65	0	0	25	----	----	----	213	11
23 [1]	23	0	53	0	0	59	----	----	----	----	----	----	----	----	----	112	14
23 [1]	23	63	0	60	0	21	39	0	0	32	----	----	----	----	----	215	14
23 [1]	23	89	0	73	----	----	----	----	----	----	----	----	----	----	----	162	5
23 [1]	23	98	0	60	----	----	----	----	----	----	----	----	----	----	----	158	5
Nov. 1	Nov. 1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	0	12
1	1	0	0	18	0	0	51	----	----	----	----	----	----	----	----	69	7
1	1	0	0	26	0	46	----	----	----	----	----	----	----	----	----	72	19
1	1	0	72	0	0	61	----	----	----	----	----	----	----	----	----	133	9
1	1	0	0	0	0	0	68	----	----	----	----	----	----	----	----	68	24
1	1	0	55	0	0	55	----	----	----	----	----	----	----	----	----	110	9
1	1	0	0	0	0	0	75	----	----	----	----	----	----	----	----	75	7
1	1	0	44	0	0	78	----	----	----	----	----	----	----	----	----	122	12
1	1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	0	10
12	13	----	----	----	----	----	----	----	----	----	----	----	----	----	----	0	5
12 [1]	13	0	0	40	60	0	0	0	0	0	17	----	----	----	----	117	15
12 [1]	13	0	0	64	53	0	0	38	----	----	----	----	----	----	----	155	11
12 [1]	13	0	41	0	24	0	0	0	0	0	27	----	----	----	----	92	11
12 [1]	13	56	0	0	47	----	----	----	----	----	----	----	----	----	----	103	5
12 [1]	13	0	57	46	----	----	----	----	----	----	----	----	----	----	----	103	8
12 [1]	13	0	0	0	0	75	----	----	----	----	----	----	----	----	----	75	16
12 [1]	13	83	65	0	49	37	0	0	0	0	25	----	----	----	----	259	11
12 [1]	13	----	----	----	----	----	----	----	----	----	----	----	----	----	----	0	16
18 [1]	18	0	0	86	0	40	----	----	----	----	----	----	----	----	----	126	10
18 [1]	18	47	60	----	----	----	----	----	----	----	----	----	----	----	----	107	2
18 [1]	18	----	----	----	----	----	----	----	----	----	----	----	----	----	----	0	10
18 [1]	18	42	----	----	----	----	----	----	----	----	----	----	----	----	----	42	5
18 [1]	18	0	55	----	----	----	----	----	----	----	----	----	----	----	----	55	5
18 [1]	18	51	28	----	----	----	----	----	----	----	----	----	----	----	----	79	5

Total eggs laid by flies ---- 17,669
Total females ---- 128
Average eggs per female (including those which did not oviposit) ---- 138

[1] In incubator at 80 to 85° F.
[2] Including 7 eggs laid on nineteenth day. No eggs were laid from the ninth day to the eighteenth day, inclusive.

TABLE 5.—*Daily mean temperatures in 1922 in laboratory at Washington, D. C., where the experiments on Piophila casei shown in Table 4 were made.*

[Based on daily average of thermograph readings taken at two-hour intervals]

Date	°F.	Date	°F.	Date	°F.	Date	°F.	Date	°F.
Aug. 29	75	Sept. 18	62	Oct. 8	75	Oct. 28	67	Nov. 17	67
30	74	19	68	9	71	29	62	18	67
31	76	20	69	10	73	30	60	19	64
Sept. 1	76	21	72	11	67	31	64	20	64
2	75	22	69	12	64	Nov. 1	68	21	65
3	75	23	70	13	65	2	68	22	63
4	79	24	73	14	68	3	68	23	66
5	80	25	67	15	68	4	68	24	66
6	80	26	62	16	69	5	69	25	66
7	80	27	65	17	70	6	68	26	54
8	76	28	68	18	68	7	69	27	64
9	77	29	70	19	67	8	66	28	65
10	78	30	70	20	68	9	67	29	67
11	79	Oct. 1	69	21	66	10	66	30	60
12	77	2	69	22	60	11	67	Dec. 1	66
13	73	3	70	23	65	12	62	2	68
14	74	4	73	24	68	13	67	3	59
15	77	5	74	25	66	14	67		
16	78	6	74	26	67	15	70		
17	70	7	73	27	65	16	67		

A general impression gained from the experiments reported in Tables 2 and 4, in which temperature was the only apparent variable of importance, is that very hot weather is not optimum for the oviposition of *P. casei.* That the mating instinct wanes during extremely hot weather has been previously noted, and the rapidity of expenditure of energy under such conditions shortens life. Larval growth, however, is most rapid during the hottest weather, as is also the process of metamorphosis within the puparium.

In Table 4 the pairs which were mated September 27 were superior in fecundity to all other groups, although the temperatures which they experienced were not unusually high. Table 6 presents a comparison of data relating to the first nine pairs mated September 27 with those of the group immediately preceding, which emerged and were mated September 4. Not enough insects are involved in this comparison to justify the drawing of conclusions, but the indications are of interest.

TABLE 6.—*Comparison of conditions influencing the fecundity of certain females of Piophila casei recorded in Table 4*

	Pairs mated Sept. 4	Pairs mated Sept. 27
Number of pairs used in comparison	8	9
Average longevity of females, in days	3.6	13.8
Minimum longevity of females, in days	3	6
Maximum longevity of females, in days	5	19
Average number of eggs laid	86	306
Minimum number of eggs laid	30	133
Maximum number of eggs laid	141	480
Average daily mean temperature (°F.)	79	69.4
Minimum daily temperature (°F.)	73	59
Maximum daily temperature (°F.)	85	79

In the records in Table 6 the two average longevities are to each other as 1 is to 3.8+ and the two oviposition averages are to each

other as 1 is to 3.6; in other words, fecundity is here very nearly in direct proportion to longevity.

During hot weather the usual reproductive period is brief. Weather sufficiently cool to delay the beginning of oviposition to the second day after mating seems to be advantageous to fecundity, since it enables more feeding prior to egg laying; and this delayed egg laying, and the lessened general activity in cool weather, apparently prolong life. In the case of the group of females mated on September 27, 1922, the cool weather continued and the temperature was such as to allow the females to have the advantage of a recuperative period after their first heavy egg laying and to develop a second series of eggs. Females which laid 200 or more eggs typically show comparatively long egg records, the eggs laid being divided more or less definitely into two groups, but hot weather usually results in the exhaustion of the vitality of the females after five or six days.

Parthenogenesis has not been observed. Virgin females seem to lay about as well as mated females but all of their eggs fail to hatch. Table 7 gives oviposition records of unmated females.

TABLE 7.—*Oviposition of virgin females*[1] *of Piophila casei at Washington, D. C., in 1922*

Female No.	Date emerged	Number of eggs laid on—								Length of life	Total eggs
		Oct. 2	Oct. 3	Oct. 4	Oct. 5	Oct. 6	Oct. 7	Oct. 8	Oct. 9		
										Days	
1	Nov. 1	77	71	31	0	0	94			6	273
2	1	0	0	0	81	25				13	106
3	1	61	50							6	111
4	1	80	36	0	33	0	0	0	41	20	190
5	1									19	0
6	1	5	53	0	0	52	0	32		16	142
7	1	0	25	0	0	0	19			21	44
8	1	0	57							16	57
9	1	0	74	0	79					7	153
Total		223	366	31	193	77	113	32	41		
Average										13.8	119.5

[1] These females were given fresh ham on November 1 and were kept at laboratory temperatures. Relative humidities in the room had little reference to the humidities in the vials, which contained moist meat. During the oviposition the daily mean temperatures were all about 70° F. None of the eggs laid by unfertilized females hatched.

Several experiments were made to determine the approximate maximum temperature at which reproduction takes place. Pairs incubated at a constant temperature of 104° F. did not reproduce, whereas those in a temperature of 102.2° F. reproduced abundantly. The indications of all trials are that the maximum temperature for reproduction lies between 102.2 and 104° F.

OVIPOSITION PERIOD AND POSTOVIPOSITION PERIOD

As is shown by the data in Tables 2 and 4, eggs are frequently laid within the first 24-hour period after mating. This is especially true of the records in Table 2 which includes records obtained in an abnormally hot summer. The first batch of eggs is as a rule larger than subsequent ones. Eggs are usually laid on three or four different days and during the oviposition period, the time from first

oviposition to the laying of the last eggs, a few days are often interspersed on which no eggs are laid. The oviposition period varies in length with the temperature, as does the postoviposition interval, but in cool weather the latter is proportionately longer than the oviposition period.

LONGEVITY OF ADULTS

The length of life of mated and fed adults was from 1 to 39 days, as shown in Tables 2 and 4. None of the unfed flies kept in a refrigerator at 48 to 50° F. lived as long as 30 days, the longest life of a fed fly in the refrigerator. The data in Table 2 show that the males usually live longer than the females.

Unmated adults kept without food or water lived as shown in Table 8. Until June 10 the weather was cool or warm, but on June 11 the daily average temperature passed above 80° F. and thereafter remained high. For this reason two divisions of the longevity records are made. The temperatures experienced by the flies included in Table 8 are given in Table 3.

TABLE 8.—*Longevity of unmated adults of Piophila casei confined without food or water at Washington, D. C., in 1921*

Died on—	Flies emerged May 19 to June 10	Flies emerged June 11 to June 22	Died on—	Flies emerged May 19 to June 10	Flies emerged June 11 to June 22
First day	3	5	Sixth day	39	0
Second day	4	95	Seventh day	6	0
Third day	103	150	Eighth day	1	0
Fourth day	222	65			
Fifth day	163	8	Total	541	323

The average longevity of the flies in the first group (Table 8) was 4.3 days and in the later group slightly less than 3 days. The average of the daily mean temperatures experienced by the flies of the first group was 74° F. and by those of the second group 81° F., the difference of 7° in the averages of the daily means being apparently responsible for the difference of over 1 day in the average lives of the insects. Temperature was the only apparent important variable.

The females used in the experiment lived longer than the males; the average female life was 4 days and the average male life 3.5 days. When pairs are mated and fed, oviposition usually results and the longevity relation of the two sexes is reversed. A summary of the longevity records of 46 such pairs (Table 2) shows that the males lived an average of 8.5 days and the females 5.1 days.

SEX RATIOS

Previous to the work included in this bulletin, the only records of the relative abundance of the sexes were published by Bachmann (*9*), who believed the males to be in the minority, and by Sakharov (*67*), who found that of 1,077 flies, 625 were females and 452 were males. The writer has observed little difference in the numbers of the sexes, but has always found a small plurality of males. Of the 864

flies shown in Table 8, 463 were males and 401 were females. Of 2,112 other flies observed (Table 9), 1,074 were males and 1,038 were females. These flies composed the entire progeny of females which laid eggs on ham in vials, each day's eggs of each individual being kept separate.

DEVELOPMENTAL PERIODS OF THE SEXES

Emergence records consistently show that the females take longer to develop than the males. Data to support this conclusion are detailed in Table 14 and also in Table 9 which follows:

TABLE 9.—*Comparative rate of emergence of the sexes of Piophila casei*[1] *at Washington, D. C., in 1921*

Sex	Number emerged on—															Total
	1st day	2d day	3d day	4th day	5th day	6th day	7th day	8th day	9th day	10th day	11th day	12th day	13th day	14th day	15th day	
Male	258	437	127	69	65	36	23	19	22	8	7	2	0	1	0	1,074
Female	18	233	351	145	82	84	38	22	25	17	12	9	1	0	1	1,038

[1] Emergence of adults resulting from daily batches of eggs laid by isolated females. Each batch of eggs was allowed to develop in a separate vial. The flies which emerged first in each vial are recorded under "1st day," the entire series being consolidated as though the beginning of emergence in all the vials had been simultaneous.

The rather long developmental periods of some of the insects recorded in Table 9 are explained by the condition of the food supply. These records were made in warm weather, when the first and last emergence of adults from a given day's eggs would have extended over only four or five days, if the larvæ had invariably had access to a plentiful supply of moist food.

BEHAVIOR OF ADULTS

The adult flies are usually eager, when confined in small glass containers, to move upward and toward the light—responses which facilitate handling them. These two responses are not particularly strong in flies which are flying freely in a room, however, and the flies are not strongly attracted to the windows, as might be expected. Unconfined flies respond principally to the stimulus of food odors. Jars containing cheese or meat, especially if these are infested with the maggots and have a decided odor, are foci for the free adult skippers in the room. Females may sometimes be observed running about over the muslin covers of the jars, feeling for apertures with their ovipositors. By placing an inverted cone in the opening of jars containing cultures of the larvæ in ham, it has been possible in the laboratory to trap numbers of the flies.

Newly emerged adults are especially attracted by odors of their foods, and it was found difficult to remove adults from a large ham riddled with galleries of the larvæ. Rather than take flight the flies preferred to dodge down into the dark interior of the meat. At another time it was found almost impossible to remove adults from a paper can, which contained thousands of puparia, both normal and empty. The attraction of the dark interior of this can was almost irresistible to the flies which had emerged in it.

In a storage room containing cured meat, flies of both sexes were always found upon the screen covering the only window, but there were more flies on the meat, even in dark corners of the room, than on the window. A few flies have been observed in the smoke chamber of an abattoir after the smoke was dissipated. The darkness of any storage room seems to be ineffective as a repellent in the presence of the overwhelmingly attractive food odors.

Mated females confined in shell vials in an incubator oviposited profusely on ham; the fact that the interior of the incubator was absolutely dark did not hinder reproduction in the least. Murtfeldt (*53, p. 174*) stated that the flies are not active at night but are able to work in partially darkened places; Kellogg (*37, pp. 114–115*) recorded flies swarming in smoky compartments; and Sakharov (*67*) believed that fish may be infested during the smoking.

In discussing the behavior of adults of *Piophila casei* it is appropriate to refer again to the interesting habit of combat between adults. This was observed by Rühl (*66*), who could find nothing similar recorded. Combat does not always appear to arise from the frenzied impulse of the males to mate; adults often spar and maul one another, apparently purely as a means of discharging their superabundant energy.

Bachmann (*9*) has given an extended account of his observations on the behavior of the flies in their fighting and mating. He observed severe fighting in which combatants were injured and even killed. Fights do not occur, he stated, in a group of flies containing only females, and the writer has made the same observation.

It is a rather common occurrence to observe adults, confined in a vial, sham death for a few seconds when the container is jarred.

THE EGG

The egg is opaquely white, very smooth and shiny, slightly curved and roundly pointed at the ends. The length is usually about 0.6 millimeter. The appearance of freshly laid eggs upon lean ham is shown at A in Figure 3.

INCUBATION PERIOD

A few observations have been made by other writers on the duration of the egg stage. Kellogg (*37, pp. 114–115*) found that eggs hatched after 4 days; Murtfeldt (*53, p. 173*), after 1½ days; Mote (*51, p. 310*) recorded incubation periods of from 23 to 54 hours; whereas Sakharov (*67*) gave the duration of the egg stage as 2 days. The writer has observed periods as short as about 23 hours, and during the hot months hatching may usually be expected after about 1 day.

HATCHING

When the egg hatches, the larva slowly works its way out of the eggshell through a small longitudinal slit in the anterior end of the egg. The empty shells collapse and are opaque, white, and conspicuous in contrast with the red color of ham.

THE LARVA

The larval stage is the most destructive and most resistant stage of the insect. It is the stage which has engaged the attention of a

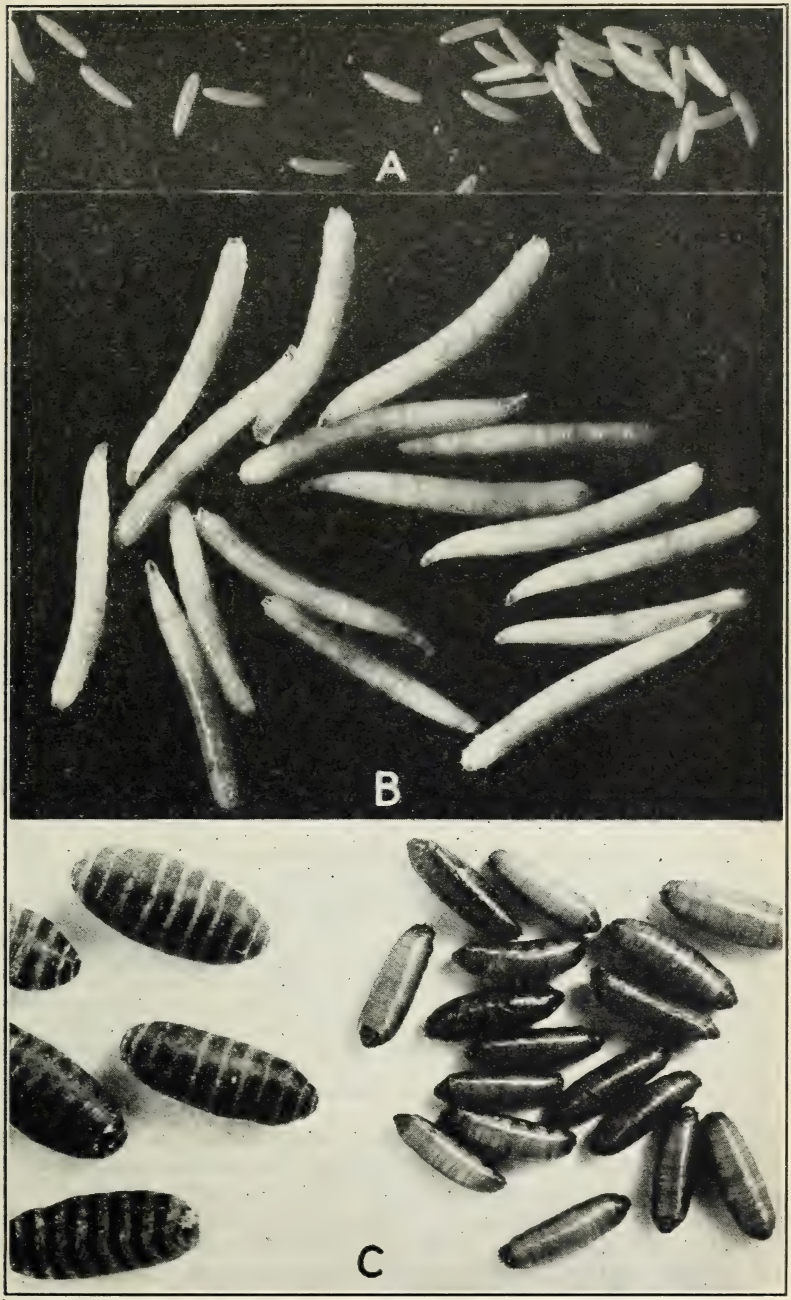

FIG. 3.—A, Eggs of *Piophila casei* on lean ham; B, Migrant larvæ of *Piophila casei;* C, Puparia of *Piophila casei* compared with puparia (on left) of *Lucilia sericata,* one of the common blowflies sometimes found infesting cured meats

number of the early writers, principally on account of the remarkable saltatorial ability displayed by the maggot. The jump of the full-grown larva has given the species its common name. The writer concludes that there are three larval instars; these have been identified by Sakharov (*67*) and by Wille (*81*).

FIRST-STAGE LARVA

The first-stage larva appears as a diminutive mass of translucent jelly. When it leaves the collapsed, flat eggshell behind, its progress is marked by a groove in the grease on the meat. Shortly after the hatching begins all the larvæ are free and soon seek the crevices of the meat, where they feed en masse. The clustering habit of these maggots is marked throughout the larval life. Larvæ transferred from one piece of meat and scattered about on another may be found the next day gathered in one or two groups. The effect of group feeding is advantageous to the individual because of the decided softening effect produced on the food. All stages of the larvæ exhibit strong negative phototropism.

As with muscoid larvæ in general, the principal taxonomic characters of the present species are the deeply pigmented oral hooks and cephalopharyngeal framework and the spiracles. A minute set of oral hooks and a very small supporting skeleton are visible in the first-stage larva, but no anterior spiracles are present; the tracheæ in the anterior region end in fine branches within the tissues. Otherwise the tracheal system is very similar to that of subsequent instars. The posterior spiracles are conspicuous.

Observation of first-stage larvæ in a shallow drop of water on dark cardboard can be made under the binocular. The principal concern of the insect under these conditions is to keep the spiracles above water, and to this end the caudal extremity of the body is kept elevated, and whenever possible the spiracles penetrate the surface film. The excrescences on which the spiracles are situated are movable at the will of the larva, which feels about with them in attempts to locate a supply of air. The writer has observed first-stage larvæ to hold the two spiracular openings in close contact with one another, evidently for the purpose of effecting a more complete closure of the respiratory system.

SECOND-STAGE LARVA

The larva of the second stage is provided with a rather slender, black cephalopharyngeal framework and slender mouth hooks. The anterior spiracles are present and consist of a pair of flat, yellow, fan-shaped processes arising between the second and third segments. Their distal edges are digitate. When closed these spiracles are withdrawn beneath the anterior margin of the third segment. The posterior pair of spiracles is very evidently the pair most used; larvæ in moist meat arrange themselves so that these breathing apertures are exposed, whereas the anterior spiracles are not usually in free contact with the air.

LARVAL SKINS

The cast skins of the first and second stage larvæ may be separated from a meat culture by vigorously dousing the infested meat in water, allowing the suspended matter to settle, pouring off most of the clear liquid, and adding fresh water. This process results in concentrating larvæ and cast skins in a small dish of clear water. In collections made in this way only two sizes of skins are found.

Skins of the first-stage larva are 1.5 to 1.8 millimeters in length, with a dorsal split at the anterior end and typically with several of the posterior segments invaginated. This infolding apparently results from the pull occasioned by the friction between the forward-moving body of the molting insect

and the posterior part of the sloughing-off linings of the tracheæ and the posterior spiracular structures. The same inpulled condition is typical of second-stage skins.

To the anterior extremity of first-stage skins a flagellum-like appendage usually adheres. This probably consists of the gut lining, and appears to inclose the cephalopharyngeal skeleton. The anterior end of the first-stage skin also bears a pair of two-jointed, fleshy antennæ and a pair of minute, indistinct areas bearing four or five dark spots which the writer assumes to be structures functioning as eyes.

The second-stage larval skin, about 4 millimeters in length, lacks the whip-like appendage of the first-stage skin, but has a pair of prominent, slender mouth hooks and a delicate cephalopharyngeal skeleton. The antennæ and eye spots are present in all stages.

THIRD-STAGE LARVA

The third-stage larva, when full-grown and ready to migrate from its food in search of a pupation place, is about 6 to 8 millimeters long, the ultimate size depending on food and environment. There are 12 segments, including the head. This stage has a robust cephalopharyngeal framework and strong mouth hooks, and is whiter and more opaque than the preceding stages.

The tracheal system is clearly visible in specimens immersed in a liquid, the confined air giving it the appearance of being filled with mercury. Both pairs of spiracles are yellow; the posterior ones are provided with conspicuous yellow, bulbous bases or stigmatic chambers. The ends of the spiracles are very small and the pattern of the openings (three oval apertures) is not easily seen. The tracheal system of the full-grown larva, seen from the side, is shown in Figure 4. The two halves of the tracheal system are joined dorsally by commissures, of which the first and last are of greatest diameter.

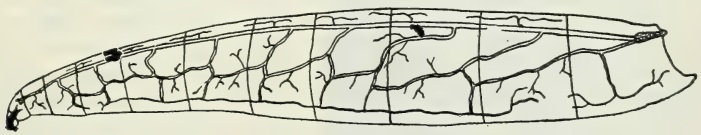

FIG. 4.—Tracheal system of migrant larva of *Piophila casei*. Left-hand half of system shown. The dorsal tracheal trunks are joined by commissures; these are not visible from the side. × 10

The modes of progression of the mature larva are two: Skipping, and creeping along by peristaltic movements of the body wall, aided by transverse rows of ambulatory teeth on the ventral surface of the last seven intersegmental lines and at the anus. The microscopic ambulatory teeth are triangular in shape, are directed posteriorly, and are arranged in triple rows, except at the anal region where only a few teeth are present.

The skip frequently propels the maggot 10 inches horizontally or 6 inches vertically. As Swammerdam (*73, pp. 63–64*) tersely expressed it, "the worm leaps with a surprising violence," and it is "surprisingly strong, and has a most vigorous constitution." In skipping, the insect bends its body in the shape of a ring and hooks its oral claws over the sharp angle formed by the ventral edge of the posterior beveled truncation. The larva then pulls hard, so hard that the two halves of the body are brought together by the strain, and the hold is suddenly released, the resulting snap throwing the insect into the air. The act is comparable to the behavior of a strip of whalebone when the two ends, which have been held together, are released. The process of adjusting the hooks is deliberate, the larva using considerable care in placing them before the strain is brought to bear. Although the skip is useful when the larva is alarmed and

is also employed in the course of undisturbed migration, the most usual and reliable method of locomotion is by creeping. This always brings the insect to a dark spot, if obstructions do not prevent, whereas the leap is haphazard and is as likely to throw the insect toward the light as toward the shadow.

Wille (*81*) has made a study of the modes of larval progression. He stated that locomotion by springing occurs in third-stage larvæ only, and is most pronounced within one day of pupation.

A photograph of larvæ of *Piophila casei* is reproduced in *b* of Figure 3. In Figure 5 is a comparison of the appearance of skippers and the larvæ of *Lucilia sericata* Meig., one of the common blowflies.

INSINUATING ABILITY OF THE MAGGOTS

An outstanding attribute of the larva is its remarkable insinuating ability. Being pointed anteriorly, slender, and very strong, it is able to enter exceedingly small crevices and therefore is difficult to confine. Petri dishes and jars closed with muslin secured by tight rubber bands do not confine the larvæ. When masses of larvæ crowded together have moistened the muslin covers of the jar containing them, some are able to force their way through the close weave of a good grade of cloth. Six layers of cheesecloth have failed to prevent the escape of the maggots from glass containers. The most effective container is a paper can, which absorbs the moisture from the surface of the larvæ, making it impossible for them to mount the sides. In glass vessels the efforts of hundreds of larvæ to escape soon coat the surface with a thin oily film, which enables the maggots to cling to the glass.

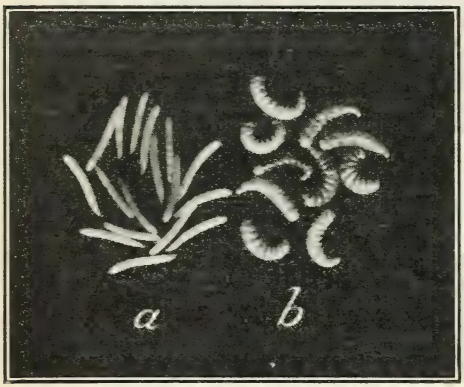

FIG. 5.—Larvæ of *Piophila casei* (*a*), compared with larvæ of *Lucilia sericata* (*b*), one of the common blowflies. Slightly enlarged

The penetrating power of the larva is useful to it in forcing its way among the layers of connective tissue between the muscles, and accounts for the depth at which maggots are found in recently infested meat. The ability of the newly hatched larva to enter a small aperture may at times lead to infestation of wrapped meat in cases where eggs are laid on greasy spots on the outside of the wrapper.

FACTORS RETARDING GROWTH OF LARVÆ

Normally the two principal influences which inhibit larval development are low temperature and starvation. The former is discussed in some detail later in this bulletin under "Control measures," and the influences of both are referred to in the consideration of the life cycle (pp. 30–34). Starvation results ordinarily from the desiccation

of food; seldom because of its exhaustion. The usual clustering habit is exhibited on dry food, but in the case of dry meat the food resists the agency which enables the maggots to soften cheese, and the larvæ become quiescent and develop alate margins on account of impoverishment. Under such adverse conditions, however, their hold on life is extremely tenacious, and even in midsummer they are able to resist starvation for weeks, and when moistened with a few drops of water become active at once.

It is worth while to note that masses of well-grown larvæ, which often congregate in the lower part of culture dishes, give rise to heat. In one case the bottom of a glass dish containing several thousand maggots clustered in a moist mass was found to be 13° warmer than the room temperature of 69° F.

The entire larval stage requires, under optimum conditions, but five days for completion. Unfavorable food and temperature conditions lengthen this period; in one case a starved larva lived for over six months, from October 2 to April 7, after which it pupated and became adult. Pavloski (*56*) reported that the larvæ have lived confined in a corked test tube without food for eight months, and later pupated.

MIGRATION OF THE MATURE LARVA

It is during migration that the insinuating ability of the skipper and its leaping powers are particularly useful. Like many other dipterous larvæ, the full-fed larva of *Piophila casei* is impelled by a strong instinct to leave the food and gain a dry, dark, close location. Of these three specifications, closeness is least important and darkness comes next, whereas dryness and freedom from grease are nearly always matters of necessity. When darkness and dryness are provided, closeness in the form of a tight crevice is sought for in addition. According to the writer's observations, puparia are formed somewhat more readily in darkness than in the light, but in hot weather, even when light was provided without interruption, the rapidity of pupation of both illuminated larvæ and those in darkness was such that the difference between them was negligible.

The behavior of full-grown larvæ which are prevented from leaving the greasy medium in which they developed is of much interest. This situation retards pupation or, if the grease is abundant, prevents it and the larvæ become quiescent. There follows a prolonged period of rest during which the insect literally has nothing to do with the exception, perhaps, of restoring slight metabolic losses by occasional feeding. Cold likewise retards or prevents pupation. At 45° to 50° F. pupation does occur, but slowly and irregularly, and many larvæ do not pupate for weeks. When hundreds of migrant larvæ are placed together in a dry container at room temperatures, the mass of maggots keeps in constant motion from the futile efforts of each individual to skip or crawl away, and this condition likewise retards pupation. When larvæ which are held in greasy or cold locations are removed to favorable surroundings, pupation takes place promptly.

In the case of a certain culture reared by the writer, a number of mature larvæ were confined with their greasy food beyond the normal time for migration. Upon their removal the pupation process was so precipitate that in 35 cases the usual prepupal contraction was

forestalled by the thickening and hardening of the skins of the larvæ. From these vermiform puparia only one adult emerged. The same circumstances, in which the migrant larva is overtaken by the phenomenon of pupation before it has reached a suitable location, probably account for the occasional puparia which are found in somewhat greasy situations upon pieces of infested meat.

MIGRATION-PUPATION PERIOD

The time which elapses between the end of the feeding period and pupation is very short, often in warm weather only two or three hours. In Table 10 it will be seen that 90 per cent of the migrant larvæ pupated within 48 hours. These larvæ were confined for periods up to 24 hours within a greasy paper wrapper inclosing the meat in which they developed.

TABLE 10.—*Migration-pupation records of mature larvæ of Piophila casei at Washington, D. C., in 1921*

Number of days after cessation of feeding	Number of larvæ pupated	Number of days after cessation of feeding	Number of larvæ pupated
1 and 2	34,314	10	1
3	3,053	11	2
4	129	15	1
5	40	16	1
6	17	20	1
7	9		
8	5	Total	[1] 37,579
9	6		

[1] In addition to the 37,579 larvæ which pupated, 229 died without pupating, making a total of 37,808 larvæ used in the experiment. The migration records of these larvæ are given in Table 1.

The numbers of the puparia in Table 10 were estimated by means of a chemical balance, it having been determined by averaging a number of weighed lots that well-nourished larvæ form puparia 230 of which weigh 1 gram. Death without pupation occurred with 0.6 per cent of the larvæ.

MATAMORPHOSIS

PUPATION

Pupation occurs readily in such situations as dry earth, sawdust, cotton, dust in floor cracks, and under boxes and sheets of paper. Frequently migrant larvæ partly or wholly enter empty skipper puparia, where they transform.

Having found a suitable place for pupation the larva contracts in length, principally at each end, and increases slightly in girth, and the skin rapidly changes from waxy white through buff and pink to a rich coppery red. At first the head retains its mobility. Just at this stage the larva, if disturbed, is able to relax and again become active, but in a very short time a point is reached beyond which there is no possibility of reversal of the pupation process.

After the hardening of the skin of the last active stage of the larva, which process forms the puparium, the insect becomes for a brief period a prepupal larva. This is a sac-like transition stage.

THE PUPARIUM

The puparia of *Piophila casei* vary considerably in size, the largest ones of normal shape measuring about 5 by 1.5 mm. The color of purparia formed by well-nourished larvæ is coppery red, whereas larvæ from dried beef, dry cheese, or old ham form puparia which are smaller and golden yellow. Puparia examined ranged from 2.5 by 0.5 mm. to 6 by 1.25 mm. A gram of puparia from an old ham culture contained 482—more than twice as many as a gram of puparia formed by well-nourished maggots. Bachmann (*9*) measured the lengths of a number of puparia and arranged the results in a frequency table. The most common length was 5 mm.

The puparia are shown in *c* of Figure 3, at right. They are deeply wrinkled at either end, with fine circumferential lines marking the surface between the intersegmental constrictions. In some puparia the latter are deeply incised, whereas flattened puparia and specimens with alate margins are not uncommon. Puparia formed by larvæ which became wedged between threads of cotton were sometimes so deeply constricted by a tight strand as to be nearly severed—a condition which of course made emergence impossible.

Puparia frequently are attached to the surface upon which they rest by a minute globule, secreted at the larval anus and attaining a resinous appearance by the time the puparium is completely hardened. Threads of cotton (Fig. 6) become glued into this globule, making the disentanglement of puparia from cotton somewhat tedious. In warm, moist weather the brittle consistency of this spot disappears and it may soften enough to stretch into a short thread capable of suspending puparia beneath the point of attachment. With the puparium secured in place by means of the globule, the adult insect is probably materially aided in the struggle to emerge.

FIG. 6.—Pupa of *Piophila casei* with part of the puparium dissected away. × 10. Threads of cotton are shown glued into the resinous globule secreted at the larval anus during the process of puparium formation

THE PUPA

The pupa is inclosed in a thin, white membrane, the skin of the prepupal larva, which lines the horny puparium. The first pigment appears in the eyes, which become pink. As the time for emergence approaches the insect assumes a smoky-gray color. A pupa with part of the puparium is shown in Figure 6.

PUPAL PERIOD

At temperatures of 80 to 90° F., the pupal period occupies a minimum of 5 days. From May 10 to June 7, 1921, no pupal period less than 7 days in length was recorded in the laboratory, most of the adults emerging on the eighth day. On June 8 the first 6-day period was recorded and on the twentieth of that month the first 5-day period. Of 1,923 puparia observed from May 10 to June 19, 250, or 13 per cent, failed to produce adults. Table 11 is a consolidation of data on the pupal period. Temperatures relative to the dates of emergence from May 19 to July 16 are recorded in Table 3.

TABLE 11.—*Pupal period of Piophila casei at Washington, D. C., in 1921*

	Number of days in pupal period								
	5	6	7	8	9	10	11	12	13
Number of flies which emerged from May 10 to June 19, 1921	166	543	350	455	145	11	1	1	1
Number of flies which emerged from June 20 to July 16, 1921	166	360	29	2	------	------	------	------	------

Table 11 shows to what extent hot weather shortens the metamorphosis. The first group, including flies which emerged from May 10 to June 19, experienced moderately warm temperatures, whereas the group of flies which emerged from June 20 to July 16 were exposed to hot weather during their pupal stage. Table 12 includes other pupation data.

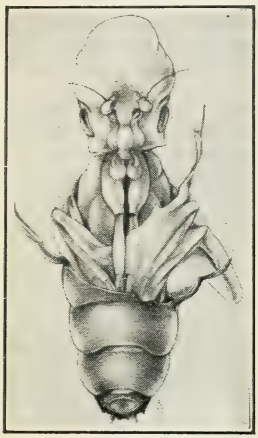

FIG. 7.—Adult of *Piophila casei* showing appearance during the act of emergence. × 10. Part of the puparium has been removed. The ptilinum is here shown at nearly maximum expansion and the pressure of the body fluids has temporarily greatly increased the size of the head

EMERGENCE OF ADULT

By vigorous use of the balloonlike ptilinum the insect forces off the dorsal half of the anterior tip of the puparium. This sometimes falls away, but more frequently opens as on a hinge and returns to its normal position after the escape of the fly. Often the dorsal and ventral halves of the anterior end of the puparium are both broken off during the fly's struggle for liberty.

The emerging fly, shown in Figure 7, rapidly becomes darker as its exoskeleton hardens. The use of the ptilinum may be observed when newly emerged flies are trying to escape from a vial plugged with cotton. The organ is greatly expanded, the force of the expanding fluid being such as to affect the whole head, displacing the eyes laterally until their inner margins are separated by an interval greater than the width of the thorax. The insect then uses its legs to push the thorax against its head, in a supreme effort to escape, the process being comparable to the driving of a wedge.

LIFE CYCLE

Table 12 summarizes available information from literature in regard to certain aspects of the biology of the cheese skipper, including facts brought out in this bulletin.

TABLE 12.—*Summary of known data on the life history of Piophila casei*

	Number of eggs	Incubation period	Larval period	Pupal period	Life cycle	Adult life	Overwintering stage
Redi, 1688 (*58, pp. 72–75*)			3 or 4 days	12 days			
Swammerdam, 1758 (*73, p. 74*)	[1] 256						
Bouché, 1834 (*18, p. 99*)				8 to 10 days			Pupa.
Taylor, 1861 (*75, p. 609*)	[2] 300						
Taschenberg, 1880 (*74, pp. 141–143*)				8 to 10 days			Pupa.
Kessler, 1883 (*38*)				12 to 14 days	28 to 35 days	8 days	Larva.
Kellogg, 1893 (*37, pp. 114–116*)		4 days	14 days	7 days		6 to 14 days	
Murtfeldt, 1893 (*53*)	[3] 30	1½ days	7 to 8 days	10 days	21 days	7 days	Adult.
Ormerod, 1900 (*54, p. 9*)				1½ to 10 days			
Howard, 1901 (*34, pp. 179–180*)					18 days		
Alessandrini, 1909 (*5*)					50 days		
Mote, 1914 (*51*)		23 to 54 hours	14 days	12 days		4 to 10 days	
Ealand, 1915 (*20, pp. 244–245*)		1½ days	14 to 15 days	10 days	21 to 35 days		
Berlese, 1917 (*11, pp. 118–121*)			8 days	12 days			
Fletcher, 1917 (*24, p. 94*)					11 days		
Bachmann, 1918 (*9*)	[4] 85		[5] 8	[5] 2			Larva and pupa.
Sakharov, 1921 (*67*)	[4] 84	2 days	20 days	8 days	30 days		Larvæ and a few newly formed pupæ.
De Ong, 1922 (*18, pp. 401–403*)		30 hours to several weeks.	8 days to several months.	7 days to 5 weeks		7 to 20 days	
Data in present paper	[4] 480	23 hours [5]	5 days [5]	5 days [5]	12 days [5]	39 days [4]	As larvæ.

[1] In ovary. [2] Nearly that number. [3] Average. [4] Maximum. [5] Minimum.

NOTE: Some of the data by other writers were obtained by rearing the insect in cheese, which is inferior to ham as a food for adults and larvæ. Temperatures of course differ greatly with locality and season, and vary from year to year. Strictly speaking, therefore, the data given above are not comparable.

Tables 13 and 14 include life-history information recorded at Washington, D. C., in the hot summer of 1921. The temperatures are listed in Table 3.

TABLE 13.—*Results of rearing Piophila casei from eggs laid in vials on juicy ham at Washington, D. C., in 1921*

Date eggs were laid	Number of eggs	Minimum period, egg to pupa	Maximum period, egg to pupa	Total puparia	Minimum period, egg to adult	Maximum period, egg to adult
		Days	*Days*		*Days*	*Days*
June 19	95	7	13	93	12	----------
19	43	8	13	13	13	----------
19	78	6	9	72	12	----------
19	93	7	11	65	12	----------
21	47	7	7	11	12	----------
23	22	8	11	16	13	----------
29	30	7	17	25	12	----------
29	128	6	10	33	12	----------
29	68	6	12	68	11	----------
30	31	6	11	31	11	----------
30	61	6	8	54	11	----------
July 20	17	7	10	16	13	----------
21	44	7	9	44	13	----------
21	70	7	15	68	12	----------
22	51	8	10	40	14	----------
23	8	8	8	2	13	----------
Sept. 2	78	6	7	69	12	13
2	72	7	9	72	13	15
2	53	7	8	33	13	14
2	66	7	9	60	13	16
2	73	6	7	71	12	15
3	63	8	11	50	14	18
3	60	7	8	56	13	17
3	63	8	17	59	15	26
3	14	7	8	14	13	15
4	36	8	9	31	14	17
9	54	9	12	30	15	20
9	60	8	13	56	14	21
9	49	8	9	41	15	17
10	54	8	9	54	14	17
10	44	7	8	40	14	18
10	37	8	12	34	15	20
12	23	9	12	20	17	21
12	31	7	8	31	15	17
12	16	10	11	11	18	19
13	19	9	11	15	17	20
16	93	10	15	87	20	26
18	68	9	23	31	19	32
18	52	10	15	52	20	26
Oct. 2	58	12	[1] 151	45	25	[1] 164
2	77	13	[1] 187	41	23	[1] 208
2	89	14	[1] 108	72	23	[1] 146
2	101	12	[1] 164	83	23	[1] 179
3	118	6	20	28	11	16
3	67	14	[1] 145	51	25	[1] 163
3	78	15	[1] 163	76	25	[1] 178
3	83	14	[1] 145	73	25	[1] 163
5	65	17	[1] 161	48	27	[1] 184
6	53	16	[1] 142	30	26	[1] 160

[1] *Approximate* duration of period in days. Development of these cultures, on account of cool weather, was slow at first, as indicated by the minimum egg-to-pupa periods, and this resulted in the food's becoming dry before the more backward larvæ had become full fed. Fresh food was provided on November 26, and on January 18 more fresh ham was given to the larvæ hatching from the 77 eggs laid on October 2 and to the larvæ hatching from the 78 eggs laid on October 3. No other attention was given except occasional brief soaking in water to separate the starving larvæ from the cavities in the hard meat. This was necessary in order that the numbers present might be recorded.

TABLE 14.—*Emergence of adults of Piophila casei from puparia formed by larvæ reared in juicy ham at Washington, D. C., in 1921*

Eggs laid / Number of eggs / Number of puparia / Number of adults	Sept. 2 78 69 68		Sept. 2 72 72 70		Sept. 2 53 33 32		Sept. 2 60 58 57		Sept. 3 63 50 50		Sept. 9 54 30 30		Sept. 9 49 41 41		Sept. 9 60 44 39		Sept. 10 37 34 33		Sept. 12 23 20 20		Sept. 12 31 31 31		Sept. 12 16 11 11		Sept. 18 52 52 52		Total 648 545 534	
Emergence dates	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Sept. 14	28																											
15	8	32	24		14	2																						
16			17	13		16	1																					
17				16			22		2																			
18							11	10	19																			
19							1	9	1	23																		
20								1		2																		
21								1		3																		
22								1																				
24													17	2	2													
25											3		5	3	8	3	6											
26											2	1		14	3	17	5	5										
27											1	3				3	1	3			4							
28											1	8			1	2	1	9			15	5						
29												10						1	6			7						
30												1					1	1	2	1			9					
Oct. 1																			3				1	1				
2																			1	6								
3																				1								
8																									1			
9																												
10																									1			
11																									8			
12																									13	6		
13																									6	13		
14																									1	3		
Total	36	32	41	29	14	18	35	22	22	28	7	23	22	19	14	25	14	19	12	8	19	12	10	1	30	22	276	258

Results of the foregoing rearing experiments show that the minimum life cycle of the cheese skipper, when provided with juicy ham as food for adults and larvæ, is 12 days, the term "life cycle" being here understood to include the preoviposition period. This brief life cycle is divided about as follows: Preoviposition period, 1 day; incubation period, 1 day; larval stage, 5 days; pupal stage, 5 days. The majority of the insects which are produced in hot weather take a day or two longer, and it is safe to say that two generations per month represents the normal rate of summer increase at Washington, D. C.

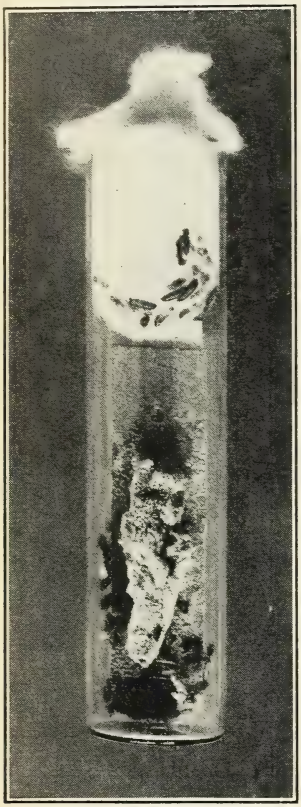

FIG. 8.—Vial used in studying the life history of *Piophila casei*, showing dead adult progeny resulting from one day's eggs laid on ham by one female. Pupation occurred in the cotton plug and emergence took place after the food was too dry to permit further reproduction

The method of rearing *P. casei* for life-history data is shown in Figure 8. In this vial one day's batch of eggs laid by one female hatched into larvæ which developed on juicy ham, migrated to the cotton and pupated there. The resulting adults died without reproducing on account of the advanced stage of drying reached by the ham at the time they emerged. This species thrives in close confinement.

INSECTS FOUND ASSOCIATED WITH THE CHEESE SKIPPER

Sakharov (*67*) has pointed out that the cheese skipper when infesting brine-cured fish has practically no competitors. The same is also true in the case of its favorite food in this country—juicy, newly cured ham. When cured meat becomes older, drier, and rancid, however, various other sarcophagous insects appear and the changes in the food medium gradually render it unfavorable for skipper development. In general, a succession of species (as suggested by Mégnin (*47*) and Stefani (*71*) with respect to cadavers) attacks cured meat as changes take place in its composition. The ham beetle (*Necrobia rufipes* DeG.) prefers meat which has been in storage for some time, and the same preference is shown by the larder beetle (*Dermestes lardarius* L.) and certain tyroglyphid mites. Skipper larvæ in freshly cured meat are sometimes accompanied by maggots of *Lucilia sericata* Meig. (fig. 5, *b*), and probably other blowflies.

In stores of bones the skipper is usually present, but in such locations the species may be at a disadvantage both because of the condition of the food supply and because of the abundance of a number of other scavengers, several of which are predacious. Skippers in heaps of bones have been found by the writer and

George W. Ellington in company with the species of insects listed below.[4]

COLEOPTERA

Dermestidae: *Dermestes lardarius* L., *D. talpinus* Mann., *D. vulpinus* Fab., *Trogoderma* sp., *Attagenus piceus* Oliv., *Anthrenus* sp.
Silphidae: *Necrodes surinamensis* Fab.
Staphylinidae: *Creophilus maxillosus* L.
Ptinidae: *Ptinus brunneus* Duft.
Tenebrionidae: *Tribolium ferrugineum* Fab., *Tenebrio molitor* L.
Cucujidae: *Oryzaephilus surinamensis* L.
Trogostidae: *Tenebroides mauritanicus* L.
Cleridae: *Necrobia rufipes* DeG., *N. ruficollis* Fab.

DIPTERA

Lucilia sp.

THYSANURA

Lepisma saccharina L.

HYMENOPTERA

Undetermined ants.

EUPLEXOPTERA

Anisolabis annulipes Lucas.

Of the foregoing, the cadelle (*Tenebroides mauritanicus*), the two species of Necrobia, and the earwig, Anisolabis, are predacious, the last three species feeding freely on live skipper larvæ in the laboratory. *Dermestes vulpinus* has predacious tendencies; a half-grown larva was deprived of other food and given migrant skipper larvæ, some of which pupated, but 10 were killed and eaten either as larvæ or pupæ within four days.

CONTROL MEASURES

There are four phases to the practice of control of *Piophila casei* as a pest in cured meat: (1) Preventing adult skippers from entering meat storage rooms, (2) preventing infestation of meats stored in rooms to which the flies have access, (3) killing skippers in infested meat, and (4) killing skippers in storage rooms.

PREVENTING THE FLIES FROM ENTERING STORAGE ROOMS

Screening is the best method for keeping the skipper flies out of storage rooms. A number of entomologists have recommended that wire cloth with 20 or 24 meshes per inch should be used for this purpose. Several trials of these sizes were made during the present investigation, and the writer concludes that wire cloth should be at least 30 meshes per inch in order to prevent passage of the flies. Table 15 gives the results of these experiments, in which puparia were placed in glass containers which were then closed with wire cloth and inclosed in a larger container. Flies which escaped through the wire cloth were counted.

[4] The writer is indebted to E. A. Schwarz and A. N. Caudell, of the Bureau of Entomology, for the determination, respectively, of several of the Coleoptera and of the earwig.

TABLE 15.—*Results of experiments in confining adults of Piophila casei with various sizes of wire cloth*

Size of wire	Number of flies	Number escaped	Per cent escaped	Remarks
20-mesh	639	183	28.6	Puparia of average size; from ham.
Do	856	263	30.7	Do.
24-mesh	1,000	1	.1	Puparia of average size; from Roquefort cheese.
Do	1,044	[1] 88	8.4	Puparia small; from Roquefort cheese.
Do	928	[2] 1	.1	Puparia average size; from beef ham.
Do	1,353	[3] 101	7.4	Puparia small; from old ham culture.
30-mesh	1,540	0	0	Do.

[1] Including 20 females. [2] Male. [3] Including 11 females.

The presence, in the vicinity of stores of cured meats, of skipper-infested bone refuse is undesirable. F. C. Bishopp, in correspondence with the writer, stated that he has advised packers "of the danger of bringing in infested prairie bones and also of storing bones about their premises, especially in proximity to cured-meat storage departments."

PREVENTING INFESTATION OF MEATS IN ROOMS TO WHICH THE FLIES HAVE ACCESS

Most common among the methods of protecting cured meats from infestation when they are hung in rooms to which the flies have access is careful wrapping of the meat. This is done in several similar ways and the wrapping may be followed, as additional protection, by a coating of whitewash or yellow wash.

As directed by Ashbrook, Anthony, and Lund (*7*, *pp. 25*, *26*), cured meat may be wrapped in heavy paper, inclosed in a muslin sack, and painted with yellow wash composed of 3 pounds of barium sulphate (barite, barytes, or "heavy spar"), 1 ounce of dry glue, 1¼ ounces of chrome yellow (neutral lead chromate), and 6 ounces of flour, for 100 pounds of hams or bacon.

Half fill a pail with water and mix in the flour, breaking up all lumps thoroughly. Mix the chrome yellow in a quart of water in a separate vessel, add the glue and pour both into the flour-and-water mixture. Bring the whole to a boil and add the barium sulphate slowly, stirring constantly. Make the wash the day before it is required. Stir it frequently while using, and apply with a brush.

Cured meat coated with yellow wash, these writers stated, should be hung up, never stacked in a pile. Before it is wrapped, the original string should be removed from each piece of meat and a new string tied tightly around the outside of the package. This is important, because it is impossible to make an insect-proof package if a string passes from the meat through the wrappings.

Special wrappings are often used to protect smoked meats to be shipped to the Tropics. These are of various colors and ingredients. A favorite protection consists of a tough though flexible coating of a black asphaltic preparation applied while warm to carefully wrapped meats.

Hams are sometimes rubbed with black pepper before wrapping. This is said to aid in preventing skipper damage by its drying action on the surface of the meat.

Borax (sodium tetraborate) is applied to the surface of cured meats by many who prepare these products for local or home consumption. This preservative is said to give protection by harden-

ing the surface of cured meats, but its use in meat products subject to the Federal meat inspection law is prohibited except in the case of shipments destined for certain foreign countries.

One of the preventive measures employed by commercial firms is rapid handling of the product; that is, meats are smoked near the retail markets and as far as possible are distributed to the retail trade promptly after the smoking is completed.

It is probable that a screened closet or cage carefully made with 30-mesh wire cloth would prove adequate and satisfactory for use on farms and in retail stores where cured meat is stored for several weeks or months. Such an inclosure would represent an initial expense only, and on farms would give protection without the necessity of wrapping and dipping meat. Screened closets in retail stores observed by the writer have been ineffective because the wire cloth used in their construction was too coarse.

But both where meats are screened and where they are wrapped the efficiency of the methods depends upon their application to hams, shoulders, and bacon which are not infested. Inspection of suspected pieces of meat can not give the assurance that they are free from eggs or larvæ of *P. casei* because the former are small and hidden in crevices by the female fly and the latter burrow so deeply that it is necessary to cut a ham in half before their favorite feeding spots can be examined.

Curing and smoking meats on farms during cool weather when the adult flies are not active is a good way to make certain that meats will not be infested before they are protected by wrappings or screens.

It has been recommended that smoked meats be wrapped and buried in a grain bin (*55*) or in sawdust or bran (*1*).

KILLING P. CASEI IN INFESTED MEAT

In the control of *P. casei* it would be desirable to be able to kill all insects and eggs in infested meat so that it can be definitely known, before shipping, wrapping, or screening suspected stocks, that they are free from infestation. This is difficult, because of the deep-seated nature of the infestations, the remarkable resistance of the larvæ, and the necessity for avoiding undesirable changes in the meat treated.

Swammerdam (*73, p. 65*) appreciated the vitality of the maggots, which when put in rain water lived for six or seven days. Curtis (*17*) decided that fumigation with sulphur was "a very doubtful remedy," and Murtfeldt (*53, p. 175*) found that this treatment impaired the appearance of sacked hams coated with yellow wash. Smith (*70, p. 368*) asserted that fumigation with tobacco or pyrethrum did not kill the maggots, although the adults succumbed. Grinnan (*29*) removed skippers from infested meat by sunning it, a process which, he maintained, brings the maggots to the surface and kills them.

TREATMENT OF LARVÆ WITH CHEMICALS AND WITH RAYS OF SHORT WAVE LENGTH

Extensive experiments with about 70 reagents as skipper larvicides have been made by Alessandrini (*4*). Chloroform he found to be instantly fatal, and death was speedily caused by immersion for one minute in carbon disulphide. He suggested the possibility of eradicating the pest in cheese factories by the fumes of chloroform, diluted with water for the sake of economy. In his experiments larvæ survived in spring water for 280 hours (nearly 12 days); in paraffin

for 38 hours, in 95 per cent alcohol for 32 hours, and in xylol for 7 hours. Ultraviolet rays (*4*) completely stopped development, whereas radium emanations merely arrested development in most cases.

Other trials of a like nature were reported in 1909 by Krausse (*40*), who used as a check for comparison specimens of an ant, *Messor structor* Ltr. His skipper larvæ were alive after 90 minutes in 96 per cent alcohol, after 301 minutes in spring water, and after 1,030 minutes in glycerine, the ants being apparently dead in each liquid after 4 minutes or less. Krausse also found that chloroform caused instant death.

Sakharov (*67*) found that infested fish may be freed of the larvæ by immersion for from 3 to 5 days in a strong brine solution, and with these results in mind he suggested that the larvæ may be successfully removed from cured meats in the same way. He tried several liquids as larvicides and found that larvæ remain alive in kerosene for 5 hours and in benzene for 10 minutes.

Trials by the writer with some common reagents agreed with the results of Alessandrini, Krausse, and Sakharov in that they show the remarkable resistance of the maggots when exposed to conditions ordinarily considered fatal to insects. However, chloroform did not give instant death. None of the materials tried gives promise of being useful for killing larvæ in meat. The requirements for this work are that the liquid be inexpensive, that it should quickly kill larvæ deep in the meat, and that it should not affect the taste or keeping qualities of the meat. Prolonged soaking, as recommended by Sakharov, or more rapid dipping would be the method used in applying a liquid for this purpose. The materials used in the experiments recorded in Table 16 are obviously unfitted for either of these purposes but the results are included in this bulletin to emphasize the unique hardihood of the maggots of *P. casei.* Following immersion, the larvæ were dried on a blotter and placed in ventilated pill boxes. The results given show that many formed puparia and that some of the pupæ had sufficient vigor to become adults. In several of the trials the skipping power of the maggots returned soon after their removal from the liquids.

TABLE 16.—*Results of immersing migrant larvæ of Piophila casei in various liquids*

Liquid used	Duration of immersion		Total larvæ used	Condition of larvæ 24 hours after removal from liquids to pill boxes			
				Dead larvæ	Live larvæ	Puparia	Remarks
	Hrs.	*Min.*					
Gasoline		30	13	0	12	1	No locomotion; slight movement.
Do	1		14	0	8	6	2 larvæ able to make some progress.
Do	1	30	15	1	10	4	6 larvæ able to make some progress.
Do	2		14	0	9	5	5 larvæ able to make some progress; 1 larva able to skip.
Do	3	15	13	1	11	1	3 larvæ able to make some progress.
Do	24		11	11	0	0	
Chloroform		1/6	9	2	7	0	
Do		1	8	2	4	2	
Carbon disulphide		1/2	5	0	5	0	
Do		1	12	2	10	0	
Do	24		9	9	0	0	
Carbon tetrachloride		20	14	5	3	6	
Ether		5	11	5	3	3	
Ethyl acetate		12	12	2	1	9	
Ammonia (concentrated solution)		34	15	2	3	10	3 of the larvæ skipping.

TABLE 16.—*Results of immersing migrant larvæ of Piophila casei in various liquids*—Continued

Liquid used	Duration of immersion		Conditions found in pill boxes after all emergence had been completed. All insects dead		
			Adults	Puparia	Larvæ
	Hrs.	*Min.*			
Gasoline		30	2	10	1
Do	1		8	4	2
Do	1	30	9	4	2
Do	2		8	4	2
Do	3	15	1	4	8
Do	24		0	0	11
Chloroform		⅙	5	0	4
Do		1	2	2	4
Carbon disulphide		½	5	0	0
Do		1	1	6	5
Do	24		0	0	9
Carbon tetrachloride		20	4	3	7
Ether		5	5	1	5
Ethyl acetate		12	3	4	5
Ammonia (concentrated solution)		34	6	7	2

The remarkable resistance of these maggots is attributed by Alessandrini (*4*) to (1) the nature of the cuticle, (2) the closure of the spiracles, (3) the amount of air held in the body and the diminished consumption of oxygen due to the immobility which they usually assume shortly after immersion, (4) the large quantity of reserve food in their bodies. Crawford (*15*) has furnished an interesting account of similar resistance by the larvæ of the ephydrid fly *Psilopa petrolei* Coq., which inhabit pools of crude petroleum.

LOW-TEMPERATURE EXPERIMENTS

Cold storage of meat is, of course, a reliable preventive of infestation, and the writer's experiments indicate that cold will kill all stages. The results of the low-temperature trials were irregular, but it is certain that speedy killing effects with cold-storage temperatures not well below freezing can not be expected. In the earliest known reference to this species (1567) Olaus Magnus (*46, p. 812*) referred to the resistance of the larvæ to cold. Murtfeldt (*53, p. 174*) asserted that "severe and protracted cold" kills all stages, and Sakharov (*67*) found that activity ceases at 8° C. (46.4° F.) and that the lowest temperature at which reproduction takes place is 13° C. (55.4° F.). The latter reported that larvæ survived—22° C. (—7° F.) for two weeks.

Oviposition trials in the laboratory resulted in the deposition of eggs by flies exposed to artificial temperatures which ranged from 56 to 62° F.

The experiments which follow show the ability of *P. casei* to resist cold.

In an ice refrigerator at 48 to 50° F.—The growth of the larvæ is suspended by temperatures of from 48 to 50° F., but under these conditions some migrant larvæ are able to pupate, and many of these pupæ produce adults and pupation is prolonged by several weeks. Eggs are not laid at these temperatures, and eggs placed in the refrigerator do not hatch. Adults are feebly active. In the case of 15 newly emerged adults placed in the refrigerator deaths began on

the sixteenth day and ended on the thirty-third day. Thirty other adults showed the first mortality on the thirteenth day and the last on the twenty-eighth day. Fifty newly formed puparia kept in the refrigerator at this temperature produced the first of 42 adults on the thirty-eighth day and the last on the forty-fifth day.

Of migrant larvæ placed in a Petri dish in the refrigerator at 48 to 50° F. on September 17, 15 were still alive on February 11, 13 were alive March 15, and 1 was alive April 17 after seven months' refrigeration. Another lot of larvæ was placed on dry sifted earth in a Petri dish October 17. A brief rise in temperature April 9 gave some an opportunity to pupate, but one was still in the larval stage May 8. Two adults emerged after June 13, showing that the insect survived at this temperature for eight months. In another test, begun January 14, in which several hundred larvæ which had been developing in a poor culture for about a month were used, 8 or 10 live adults were observed August 15.

Experiments with migrant larvæ in a refrigerator show that the duration of this stage of the insect may be considerably lengthened by certain manipulations. After such larvæ have been confined for several weeks at about 48° F., their shrunken appearance indicates that they have undergone metabolic losses, and this is further shown by the readiness with which they begin feeding again when placed on juicy ham. In a day or so the maggots again become full fed, whereupon they migrate a second time. If they are then collected at once and replaced in the refrigerator, the process may be continued, probably over a long period if the temperature is always kept low enough to prevent most of them from pupating.

In a sulphur dioxide refrigerating machine at about 32° F.—Mature puparia were exposed in a sulphur dioxide refrigerating machine at 32° F. on March 15, after having been in the ice refrigerator since March 2 at from 48 to 50° F. A sample of these puparia was removed June 3, and emergence resulted after exposure to room temperatures. This pupal period was therefore three months.

About 50 adults were exposed on February 16, having been taken from a temperature of 51° F. One of these survived until after March 15, a period of one month. In another lot of 98 flies, one survived 33 days and one lived 37 days.

Full-grown larvæ at 32° F. do not pupate. After removal to room temperatures, following refrigeration for periods up to nearly three months, puparia were formed which produced adults.

Half-grown larvæ, removed to 32° F. from a temperature of 86°, were all dead after six weeks; in another lot, with the same history, three were alive after six weeks.

Eggs refrigerated at 32° F. for periods up to two weeks hatched with hardly an exception after removal to favorable temperatures. In this test newly emerged and newly mated pairs were allowed to oviposit on ham and then the adults and eggs were placed in refrigeration. Upon removal, after progressively longer periods of exposure to cold, the adults were given favorable food and temperatures. The females which were subjected to this degree of cold for periods up to and including 10 days resumed the deposition of fertile eggs.

Eggs exposed to 32° F. for one month failed to hatch.

In an ammonia refrigerating machine at 0, 5, 10, and 15° F.—Table 17 gives results of a few experiments in an ammonia refrigerating machine at temperatures considerably below freezing. The larvæ which were able to survive the cold for periods of 44 hours or more were less than half grown; all maggots of other sizes were killed. It is interesting to note that these larvæ survived low temperatures for periods greatly in excess of the exposures which killed all stages of a variety of other species of stored-product insects which have been tested with the ammonia machines.

TABLE 17.—*Results of exposing adults, pupæ, and mixed sizes of larvæ of Piophila casei to low temperatures*

Stage	0° F.	5° F.	10° F.	15° F.	Results
	Hrs.	*Hrs.*	*Hrs.*	*Hrs.*	
Pupæ	16½				All dead.
Larvæ		16½	16½		Not all dead.
Pupæ		16½	16½		Do.
Adults		16½	16½		All dead.
Larvæ		24	24		Do.
Pupæ		24	24		Not all dead.
Adults		24	24		All dead.
Larvæ			41		Do.
Do		41			Not all dead.
Do		44	44		Do.[1]
Do		64½		208½	Do.[1]

[1] Of mixed sizes of larvæ subjected to these exposures, only specimens less than half grown survived.

A large number of full-grown larvæ were placed in an outdoor fumigating box on December 16, 1922. On February 27, 1923, several hundred were removed to room temperatures and all of them became active after about 15 minutes, and subsequently developed into adults which laid fertile eggs.

EFFECT OF HIGH TEMPERATURES

Except for the statement of Grinnan (*29*) that he was accustomed to place infested meat in the sun to kill the skippers in it, and a record by Alessandrini (*4*) that 55° C. (131° F.) was fatal in two minutes, there is no published mention of the use of heat as a control measure. At a small abattoir near Washington the resmoking of infested meat was tried with some success several years ago, but as this involves considerable labor in handling the meat, the writer attempted to raise the temperature of the meat as it hung in the storage room. The results were negative. After several hours the kerosene heaters, as expected, so exhausted the oxygen of the compartment that they were extinguished, and sufficient ventilation to allow them to burn freely kept the temperature from rapidly reaching the required point. It is possible, however, that under certain conditions steam heat may be used effectively. When the kerosene stoves were used—and their use to produce high temperatures is not safe—the reading of the thermometer at the floor, which was about 68° F. at the start was 98.5° after 15 hours of constantly rising temperature; halfway up to the ceiling it was 115°, and at the ceiling, 132°—a difference of 33.5° between floor and ceiling in a room 7 feet 6 inches high. The floor was of concrete and the walls and

ceiling plastered. Since the meat was suspended at all levels in the room, it would appear necessary to use a fan to obtain a more even distribution of heat.

The rapidity with which heat from heated air penetrates cured meat was the subject of a test in an electric oven. An 8-pound shoulder, old and rather dry, was placed in the oven at 8.35 a. m. Table 18 shows the temperatures during the test. The temperature of the room from which the shoulder was taken was 72° F.

TABLE 18.—*Data showing details of results of heating an 8-pound shoulder in an oven*

Time	Temperature of oven	Temperature of surface of meat	Temperature of center of meat	Remarks
	° *F.*	° *F.*	° *F.*	
8.35 a. m.	124			
9 a. m.	128			
9.45 a. m.	130			
10.23 a. m.	128			
11 a. m.	130			4 adults of *Necrobia rufipes* and 2 larvæ active on meat.
12 noon	128		107.6	2 adults of *Necrobia rufipes* active on meat.
12.40 p. m.	132	122	110.3	
1.05 p. m.	130	122.9	113.0	
2 p. m.	132	125.6	116.6	
2.40 p. m.	130	125.6	120.2	
3.15 p. m.	130	126.5	121.1	Several dead larvæ of *N. rufipes* on meat.
3.45 p. m.	130	126.5	123.8	
7 p. m.	136	131	128.3	

High temperature in an incubator.—Experiments with the exposure of adults and larvæ to high temperatures in a water-jacketed electric incubator were not satisfactory. When Petri dishes and cotton-plugged vials were used, the exact temperatures to which the larvæ and adults were subjected were not known, especially in the case of short exposures. The time required for the air in a stoppered 20 by 100 millimeter vial to reach oven temperature was found to be considerable. A vial removed from a room temperature of 78° F. was fitted with a thermometer passing through the tight cotton plug, the bulb being suspended in the center of the vial. This was put in the incubator where the air was 120° and a period of 30 minutes was required for the air in the vial to become heated to 118°.

In general, it is apparent that adults are killed or seriously paralyzed when confined at 120° F. for half an hour. Migrant larvæ were still active after 22 hours' exposure to 110 to 112°; they were able to skip following 69 minutes in a temperature of 120°; others formed puparia after being heated for three hours at 118 to 122°; some recovered after four hours at 122 to 124°; and larvæ became active after 40 minutes at 126 to 128° F. After allowing a liberal margin for slow heat transference, it is evident that migrant larvæ of the cheese skipper are resistant to dry air temperatures up to 124° for exposures of several hours.

Since so little is known as to the shrinkage or possible injury to infested smoked meats heated to temperatures and for lengths of time which would be larvicidal and at the same time practical to use, the writer does not recommend the use of dry heat to kill skippers in smoked meats.

High temperature in hot water.—It is possible to assemble accurate information regarding the resistance of migrant larvæ of *Piophila casei* to heat by immersing them in hot water. In experiments of this kind the only apparent variable is the heat, which can be closely regulated and which reaches the larvæ without passing any insulating barrier such as is present when maggots are exposed in vials to hot air. In Figure 9 the results of a number of trials with migrant larvæ are plotted. The position of the dots (fatal immersions) and circles (immersions not fatal 24 hours after removal from the water) defines the approximate location of a mortality curve for this species.

Each test shown in Figure 11 was made by holding about 10 larvæ in a coarse strainer immersed in several gallons of water. Inasmuch as immersion in water of room temperatures has no effect on the

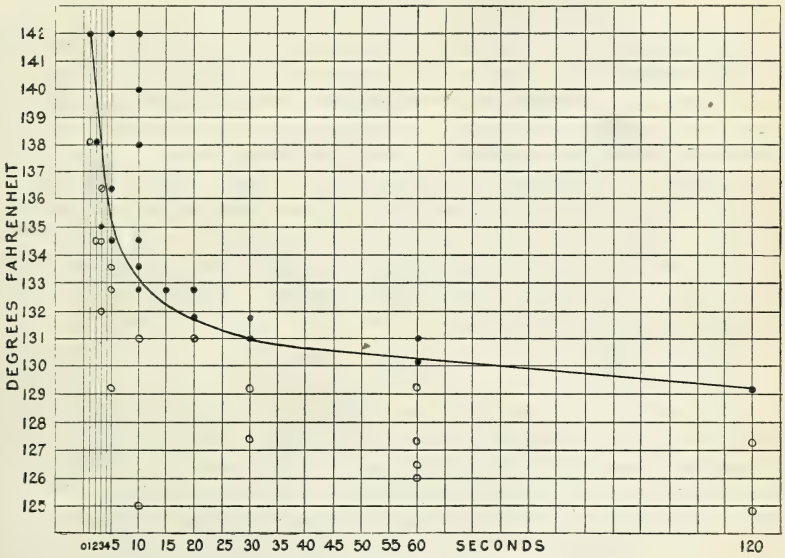

FIG. 9.—Mortality curve for migrant larvæ of *Piophila casei* immersed in hot water. The dots represent experiments in which all were dead 24 hours after immersion; the circles indicate trials which resulted in either continued activity or metamorphosis at the end of 16 days; the tests which were not fatal after 24 hours but which showed 100 per cent mortality after 16 days are shown as circles crossed by a diagonal line

larvæ even if continued for two or three hours, the drowning action of the water in the tests is not considered to be the primary cause of death.

Hot water transfers heat to meat more rapidly than does hot air, but in attempting its use as a skipper larvicide two possibilities must be guarded against—leaching the meat and cooking it. The temperature should be high enough to provide for a brief though fatal period of immersion, yet not so high as to produce a noticeable cooking effect.

According to information compiled by the meat inspection division of the Bureau of Animal Industry, commercially cooked hams are not usually boiled but are cooked at temperatures as low as 155° F., a temperature of about 170° being commonly used. It is evident, then, that the maximum useful temperature for killing skippers in

smoked meats which are to be stored uncooked is rather low, probably less than 150°.

Trials by the writer with shoulder butts weighing about 2 pounds each show clearly that the period of hot-water immersion necessary to heat the center of even small pieces of meat to a lethal temperature would be impracticably long, even with water temperatures which would result in some cooking. With protracted hot-water immersion there would not only be danger of leaching the meat but the attention required to keep the temperature nearly constant would be so considerable that the method does not seem to be applicable.

Dipping cured meats in boiling water will not reach maggots buried in the tissues unless immersion continues long enough to cook the surface.

FUMIGATION WITH HYDROCYANIC-ACID GAS

In the summer of 1920, E. A. Back, in charge of stored product insect investigations, Bureau of Entomology, in cooperation with R. H. Kerr, in charge of laboratories, meat inspection division, Bureau of Animal Industry, undertook some experiments with hydrocyanic-acid gas against *P. casei* in cured meats. The unpublished results of the analyses of fumigated meat, made under Kerr's direction, showed that acid taken up by the meat during fumigation was very rapidly dissipated when exposure to the gas was discontinued, and that none of the acid was retained. Following these experiments, the Bureau of Animal Industry authorized the use of hydrocyanic-acid gas for fumigating meats in establishments subject to Federal regulation (*78*).

Griffin and Back (*28*) subsequently published analyses of cured meats which had been fumigated with the gas, using a dosage of 1 ounce of sodium cyanide per 100 cubic feet. These results showed that some of the acid was absorbed and that small quantities were retained for several days, but no conclusions were drawn regarding the safety of such fumigated meats for use as human food.

The writer has used this method of treating infested cured meats, usually with dosages of about 2 ounces of sodium cyanide for each 100 cubic feet of space. No ill effects have been experienced from the consumption of meats thus fumigated, which were largely disposed of by sale to employees of the Bureau of Animal Industry in Washington. The safe use of such fumigated meats probably depends upon airing them for several days after exposure to the gas and upon the fact that they are cooked before being consumed.

Hydrocyanic-acid gas, used as stated above, causes very high mortality among skipper maggots, but a dosage of 2 ounces of sodium cyanide per 100 cubic feet is not always to be depended upon to kill all of those which are deep in the tissues of meat. On one occasion about 25 hams and shoulders were examined after having been exposed to the gas from Saturday afternoon to Monday morning. Hundreds of skippers had crawled to the surface of the meat and died there, and small heaps of dead maggots had accumulated on the floor beneath some of the heaviest infestations, but inspection revealed live larvæ in nearly all of the pieces of meat.

Eggs exposed at 70 to 80° F. to a dosage of 1 ounce of sodium cyanide per 100 cubic feet for 24 hours were all killed. Adults,

pupæ, and unprotected larvæ have been killed by exposure to the same dosage for 23 hours, during which period the temperature fell from 65 to 55° F.

Any process used for killing skipper maggots in cured meats should of course be followed by cutting out infested parts.

KILLING PIOPHILA CASEI IN INFESTED ROOMS

According to Murtfeldt (*53, pp. 174–175*) the fumes of burning sulphur or pyrethrum powder kill the adults. One firm with which she corresponded whitewashed infested rooms after fumigation, using carbolic acid in the whitewash. Howard (*32, p. 104*) suggested that infested places be washed with kerosene emulsion, special attention being given to the cracks. Burning sulphur or pyrethrum on live coals kills the flies if rooms are kept closed for from 8 to 24 hours (Smith, *70, p. 368*), but as this does not kill the maggots it should be repeated. Smith also believed that carbon disulphide could be used with good effect.

Surface (*72, pp. 21, 24*) suggested that badly infested rooms be fumigated with hydrocyanic-acid gas, and Herrick (*31, p. 292*) directed that such rooms be washed with kerosene oil.

The writer found that strong dosages of pyrethrum powder or of pyrethrum smoke almost completely paralyzed the adults after 10 to 15 minutes, and that death followed in about 2 days. Measurements of the dosages used were not attempted. Migrant larvæ were placed in a mass of pyrethrum powder which was taken from a freshly opened air-tight bottle, and 2 days later 22 of the 29 larvæ had pupated in the powder. Eighteen of these puparia produced adults.

Carbon disulphide, at the rate of 1 pound per 100 cubic feet for 20 hours, was tested as an insecticide for all stages. The temperature was about 75° F. and the relative humidity ranged from 86 to 98 per cent. Some of the larvæ (migrants) were not killed, but there was no emergence from the puparia exposed to the gas. No progeny developed from the eggs, and the adults were all killed.

The vapor of carbon disulphide is inflammable and highly explosive when mixed with air in certain proportions. There must be no fire, or sparks of any kind, where fumigation is being carried on.

Sulphur fumigation has been extensively used in the past for the control of various insects, but it has now been largely superseded by other fumigants, chiefly on account of its strong bleaching and tarnishing action in the presence of moisture and its harmful effects on growing plants and on the germinating power of grain. Records of the use of this fumigant against insects indicate that the method has generally been effective. Although sulphur fumigation tests with *P. casei* were not made in this investigation, it is probable that strong fumes are fatal to this species except when the larvæ are imbedded in the tissues of meat. In tight compartments an effective concentration of the gases from burning sulphur appears to be obtained by the use of about 3 pounds of stick sulphur per 1,000 cubic feet of space, with exposure for 24 hours.

The most reliable method of treating infested rooms is thorough sweeping followed by fumigation for 24 hours with hydrocyanic-

acid gas, using at least 2 ounces of sodium cyanide per 100 cubic feet.

Since hydrocyanic-acid gas is very poisonous to human beings when it is inhaled, its use in occupied buildings or in locations where the gas may leak through into adjoining occupied buildings should not be attempted. Only careful persons thoroughly informed as to the proper methods of procedure should undertake to generate this gas. After fumigation, rooms must be thoroughly ventilated before being entered.

On account of the uncertainty which attends attempts to kill all the maggots that are deep in the tissues of infested meats, it is suggested that infested stocks be removed from storage spaces from which it is desired to eradicate the insect.

NATURAL ENEMIES

Indefinite reference to a parasite of *Piophila casei* was made by Swammerdam (*73, p. 69*), Taylor (*75, p. 609*), and Fletcher (*24, p. 94*). In the summer of 1921 the writer reared from pupæ of the cheese skipper numbers of a pteromalid parasite (Hymenoptera), identified by A. B. Gahan of the Bureau of Entomology as *Pachycrepoideus dubius* Ashmead. Records of the distribution of this parasite include Illinois, the Philippine Islands, Hawaii (introduced), Canada, and eastern Australia. It is an enemy of a number of Diptera, notably the house fly (*Musca domestica* L.). In Hawaii, where it is also a parasite of the Mediterranean fruit fly (*Ceratitis capitata* Wied.), it has been introduced from the Philippines, propagated, and liberated as a parasite of the horn fly (*Haematobia irritans* L.), and in 1910 it was reared in Canada from a breeding jar containing the puparia of the cabbage root maggot (*Hylemyia brassicae* Bouché). In Australia it parasitizes various sheep-maggot flies. The records do not indicate ability on the part of *P. dubius* to make an important contribution to the control of any of its hosts, and there is small probability that it will ever be of much assistance in the control of the cheese skipper.

In the laboratory in the summer of 1921 a minimum period of 16 days elapsed between the exposure of skipper puparia to oviposition by *P. dubius* and the emergence of adult parasites. As a rule only one parasite developed in each puparium, but three puparia produced two parasites each. Three females, which emerged September 9 and reproduced, and which were not fed, lived respectively 9, 9, and 13 days.

Several insect associates of *P. casei* prey upon it. Chief among these is the clerid beetle *Necrobia rufipes* DeG. (the ham beetle), which is predacious both as adult and larva. Young larvæ of *N. rufipes* are unable to kill migrant skippers, but vigorous migrant skipper maggots are readily killed by larger larvæ of this beetle, and in rearing experiments with the latter skippers have been found to be the best food for larvæ and adults. Table 19 shows the predacity of this beetle, which is also cannibalistic. In the laboratory, colonies of skippers to which these beetles had access were observed to be rapidly depleted. Adult ham beetles also have eaten skipper eggs, dead adults, and puparia.

TABLE 19.—*Results of exposure of migrant larvæ of Piophila casei to larvæ and adults of Necrobia rufipes*

Number of *P. casei* larvæ exposed	Number of *N. rufipes* used	Stage of *N. rufipes* used	Predacity record after 24 hours
			Per cent
20	4	Full-grown larvæ	0
20	2	do	0
20	4	do	0
20	2	do	40
20	3	Half-grown larvæ	55
20	3	do	70
20	2	Adults	45
20	4	do	85
20	2	do	50
20	4	do	75
20	9	Adults	60
	3	Full-grown larvæ	
20	9	Adults	100
	3	Full-grown larvae	
20	12	Adults	90
	6	Half-grown larvæ	

Adults of *Necrobia ruficollis* Fab., sometimes found in material infested with *P. casei*, are also actively predatory upon these maggots. *Pediculoides ventricosus* Newp., a widespread predacious mite, rarely kills the larvæ and flies.

SMOKEHOUSE CONDITIONS

A variety of types of smokehouses are in use, ranging from chambers the size of a barrel, through the usual wooden or masonry farm smokehouse, to the improved apparatus used by the larger packers (*3, pp. 98–102*). Some of the improvements in the last class include automatic temperature control, auxiliary heat supply from steam pipes, and gas fuel for burning the smoking sawdust. Some smoke chambers are arranged for continuous operation, the meat being carried up and down during the smoking on a chain conveyor and removed while hot to the hanging room as soon as sufficiently smoked.

The duration of smoking varies from a minimum of about 24 hours for sweet-pickle hams prepared for a market which desires meat with a high water content, to light, intermittent smoking for five or six weeks as in the preparation of Smithfield hams. The best smoking temperature is about 120° F., but as a usual thing there is considerable variation from an even, optimum heat.

The time during which cured meats remain in the smokehouse may be divided for purposes of discussion into two parts. The first period, in which the danger of infestation is comparatively small, begins when the meat, wet from soaking and washing following cure, is hung in the smokehouse to dry, and ends when the heat of the fire drops for the last time below 100° F. The second period, during which, in warm weather, infestation is certain in localities where skippers are found, begins when the first period ends and lasts until the meat is removed from the smokehouse.

After having been washed and hung in the smokehouse, meats need to dry about three hours before the fire is lighted. In view of the fact that dry-salt pork (unsmoked) is sometimes infested, it is

very probable that eggs are occasionally laid on cured meat while it is drying in the smokehouse. There follows the question as to whether any eggs so laid, or laid in times of favorable temperatures during intermittent smoking, can survive the subsequent high temperatures, heavy concentration of smoke, and smothering effect of melted fat. Nothing very definite can be said with respect to this point, principally on account of the lack of uniformity in the degree and duration of the heat produced. In some cases (fig. 10), the heat would be expected to kill any adults, eggs, or young larvæ which might be present.

Throughout the warm months it is clearly apparent that one of the most important flaws in our defense against skipper infestation consists in the commonly unprotected condition of smoked meat dur-

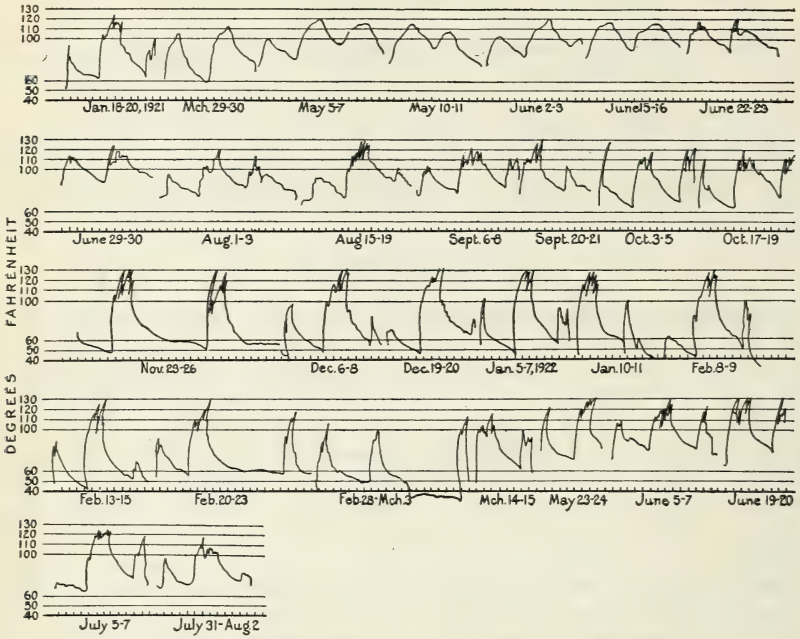

FIG. 10.—Reproductions of thermograph records of smokehouse temperatures. The scale marked on the 40-degree line measures 4-hour intervals

ing the second part of its stay in the smokehouse. From the time the heat drops below 100° F. for the last time until the meat is removed from the smokehouse there is a period of temperatures favorable to egg laying. The above diagram (fig. 10) gives a number of smokehouse records [5], with the approximate range of reproductive temperatures shown by the wide interval between 60 and 100° F.

As shown in this diagram, there was usually abundant opportunity, so far as temperatures were concerned, for the flies to oviposit

[5] Pantograph copies of thermograph records obtained through the interest and courtesy of E. Z. Russell, in charge of swine investigations, Animal Husbandry Division, Bureau of Animal Industry. The writer is also indebted to K. F. Warner, of the swine investigations, and to G. A. Anthony, inspector, Washington Center Market, Bureau of Agricultural Economics, for valuable cooperation in many ways.

on the meat after the last record of a temperature of 100° F.; that is, during the second period. But the ends of these records did not always coincide with the removal of the meat from the smokehouse; the thermograph was frequently taken from the smokehouse hours before the meat was removed.

Wilder and Davis (*79, p. 366*) directed that the fire should be put out when the smoking is completed, the house opened up, and the meats allowed to cool. These writers realized, however, the danger of exposing meats in unprotected smokehouses, and recommended (*p. 371*) that the windows and doors be finely screened, and that smokehouses should be regularly fumigated with sulphur.

While smoked meats are cooling off in the smokehouse, they are not only at maximum attractiveness for skipper flies but also readily accessible to the flies when unscreened doors, windows, or ventilators are left open. The writer has observed skipper flies upon meats in the smokehouse at this stage, and recommends that the houses be of tight construction and thoroughly screened with wire cloth of at least 30 meshes per inch.

SUMMARY AND CONCLUSIONS

Piophila casei (L.), a piophilid fly commonly known in its larval or maggot stage as the cheese skipper and ham skipper, and by other popular names, is widely distributed throughout the world. In the United States it is the chief insect pest in smoked, cured pork, and cheese. It is able to nourish itself in dried beef, salt pork, cured fish, and a variety of inedible animal products.

Medical literature contains records of myiasis caused by the presence of skipper larvæ in the intestines, a condition which probably not infrequently results from the custom of eating infested cheese. There are several published accounts of the presence of this species in exposed human corpses and its remains have been found in graves.

The characteristic injury done to cured hams and shoulders consists of eaten-out areas among the large muscles, and these extend to the center of the meat, close to the bones. Very fat meat, such as bacon, is not extensively injured; the insect prefers connective and muscular tissue.

The adult is a very active, small, tame, shining black fly somewhat resembling a winged ant. It feeds principally on the juices of the larval food, and liquid or semiliquid food is a prerequisite to normal oviposition.

Fertile eggs are laid as soon as 10½ hours after the act of mating, the latter often taking place a few minutes after the female leaves the puparium. Unmated females deposit infertile eggs. The eggs are rapidly scattered about over the surface of the meat or masses of them are concealed in crevices. The maximum number of eggs laid by one female is nearly 500, but the usual number is about 140, laid over a period of three or four days.

Flies kept at low temperatures (48 to 50° F.) may live for more than a month. During hot weather (80 to 90° F.) the usual length of life is three or four days if food and water are not provided. When flies are unfed the females live longer than the males; the

reverse is true when they are fed and mated. In midsummer males in breeding vials lived an average of 8.5 days and females 5.1 days.

Male flies are slightly more numerous than females and they usually require less time for metamorphosis. Both sexes are attracted to light, but this stimulus is not a dominant one in the presence of food odors.

The eggs hatch in about 24 hours at 80 to 90° F. and the larvæ cluster together for feeding. There appear to be three larval instars. All stages of the larvæ are repelled by light.

After the completion of feeding the full-grown larva leaves its food and seeks a dark, dry spot for pupation. The larval and pupal stages are each five days long in hot weather (80 to 90° F.) when fed on juicy ham. The life cycle occupies a minimum of 12 days, and at Washington the average rapidity of summer increase is two generations per month. The range of temperatures at which reproduction takes place is approximately 56 to 102° F.

Control suggestions come principally under four heads:

1. Preventing adults from entering storage rooms. This may be accomplished by careful screening with 30-mesh wire cloth and by using care that flies do not enter when the doors are opened.

2. Preventing infestation of meats in rooms to which the flies have access. The usual method consists of wrapping each piece of meat in paper and inclosing the whole in a tight cloth sack, often with a coating of yellow wash as additional protection. On farms and in retail stores a closet or cage with sides of 30-mesh wire cloth should be provided for the storage of cured meat. On farms, such a cage would render wrappings, sacks, and washes unnecessary. The prevention of infestation is the essence of skipper control.

3. Killing *Piophila casei* in infested meats. The maggots are very difficult to kill, especially when they are feeding in the moist interior of pieces of meat. They are able to withstand extremes of temperatures, starvation, and immersion in water and other liquids for periods which would be fatal to most insect larvæ. Hydrocyanic-acid gas fumigation causes heavy mortality among skippers in meat, but even strong dosages are not certain to kill them all. Inspection of suspected hams and shoulders can not be relied upon to disclose either the minute, concealed eggs or all of the deep-seated feeding larvæ.

4. Killing *Piophila casei* in infested rooms. To kill all stages nothing is better than strong dosages of hydrocyanic-acid gas (2 ounces of sodium cyanide per 100 cubic feet) applied for 24 hours.

On account of the large number of skippers which may be produced by a single piece of meat, it is advisable to destroy promptly all infested meat which can not be reconditioned by trimming. Supplies of bones should not be allowed to accumulate near stores of smoked meats.

Where curing and smoking operations are confined to the winter months, in parts of the country where the temperatures are below the minimum reproductive temperature of the skipper (about 56° F.) the danger of early infestation is avoided.

Smokehouses should be well screened. Meats stored in a well-screened farm smokehouse should require no further protection of any kind.

The biology of *Piophila casei* reveals no excuse for neglecting, during the skipper-fly season, to protect cured meats with fine screens, glass cases, or low temperatures from the time they leave the curing vats until they are either wrapped or rapidly carried through trade channels to the consumer. There may be economic reasons for avoiding the expense of protection, and in each case the risk of loss through skippers should be balanced against the cost of preventing such damage.

LITERATURE CITED

About 170 references to *Piophila casei* are to be found in the literature of entomology. A few more than half are omitted from the following pages because they largely duplicate previously published data.

Illustrations of the insect which are especially worthy of note are to be found in papers by Alessandrini (*5*), Banks (*10*), Dufour (*19*), Mote (*51*), Sakharov (*67*), and Swammerdam (*73*, *pp. 63–75*).

The principal contributions to the biology and control include: Alessandrini (*4*, *5*), Bachmann (*9*), De Ong and Roadhouse (*18*), Howard (*32*), Kellogg (*37*, *pp. 114–115*), Kessler (*38*), Krausse (*40*), Mote (*51*), Murtfeldt (*53*), Ormerod (*54*), Redi (*58*), Sakharov (*67*), Swammerdam (*73*), Willard (*80*), and Wille (*81*).

(1) Anonymous.
1891. weevils in bacon. Agr. Gaz. N. S. Wales 2: 557.

(2) ———
1896. case of larvae in the nose. Shown by Dr. J. W. Bond. Jour. Laryngology, Rhinology, and Otology 10: 236–237.

(3) Aldrich, P. I.
[1922]. the packers' encyclopedia. 529 pp., illus. Chicago.

(4) Alessandrini, G.
1907. sulla resistena vitale sulle larve della piophila casei l. Bol. Soc. Zool. Ital. (II) 8: 374–380.

(5) ———
1909. studi ed esperienze sulle larve della piophila casei. Arch. Parasitol. 13: 337–382, illus.

(6) [American Association of Economic Entomologists.]
1925. common names of insects approved for general use by the american association of economic entomologists. Jour. Econ. Ent. 18: 521–545.

(7) Ashbrook, F. G., Anthony, G. A., and Lund, F. P.
1921. pork on the farm. killing, curing, and canning. U. S. Dept. Agr. Farmers' Bul. 1186, 44 pp., illus.

(8) Austen, E. E.
1912. british flies which cause myiasis in man. [Gt. Brit.] Local Govt. Bd., Rpts. Pub. Health and Med. Subjs. (n. s.) 66: 5–15.

(9) Bachmann, M.
1918. biologische beobachtungen über die käsefliege. Ent. Ztschr. 31: 93–94, 99–100, 101–102; 32: 1–2, 5–6, 10–11, 14–15, 19–20, 23–24, 27, 30–32.

(10) Banks, N.
1912. the structure of certain dipterous larvæ with particular reference to those in human foods. U. S. Dept. Agr., Bur. Ent. Tech. Ser. 22, 44 pp., illus.

(11) Berlese, A.
1917. insetti delle case e dell'uomo e malattie che diffondono con particolare riguardo al modo di difendersene nelle città, nelle campagne, al fronte. 293 pp., illus. Milano.

(12) Bishopp, F. C.
1917. some problems in insect control about abattoirs and packing houses. Jour. Econ. Ent. 10: 269–277, illus.

(13) Bouché, P. F.
1834. naturgeschichte der insekten, besonders in hinsicht ihrer ersten zustände als larven und puppen. Lfg. 1, illus. Berlin.
(14) Colombe, J., and Foulkes, D.
1924. myiases du tube digestif. Lancette Franç.; Gaz. Hôpitaux Civ. et Mil. 97: 5. [Not seen.]
(15) Crawford, D. L.
1912. the petroleum fly in california, psilopa petrolei coq. Pomona Coll. Jour. Ent. 4: 687–697, illus.
(16) Curtis, J.
1826. british entomology. vol. 3, illus. London.
(17) ———
1855. piophila casei (linn.). *In* Morton, J. C., A Cyclopedia of Agriculture, vol. 2, p. 611, illus. Glasgow, Edinburgh, [etc.].
(18) De Ong, E. R., and Roadhouse, C. L.
1922. cheese pests and their control. Calif. Agr. Expt. Sta. Bul. 343: 399–424, illus.
(19) Dufour, L.
1844. histoire des métamorphoses et de l'anatomie du piophila petasionis. Ann. Sci. Nat., Zool. (3) 1: 365–388, illus.
(20) Ealand, C. A.
1915. insects and man: an account of the more important harmful and beneficial insects, their habits and life-histories, being an introduction to economic entomology for students and general readers. 343 pp., illus. New York.
(21) Fabricius, J. C.
1775. systema entomologiae. 832 pp. Flensburgi et Lipsiae.
(22) ———
1805. systema antliatorum. 372 pp. Brunsvigae.
(23) Fallén, C. F.
1820. heteromyzides sueciae. 10 pp. Lundæ.
(24) Fletcher, T. B.
1917. report of the imperial pathological entomologist. Agr. Research Inst., Pusa, Sci. Rpts. 1916/17: 91–102.
(25) Frisch, J. L.
1730. beschreibung von allerley insecten in teutsch-land. Theil 1, illus. Berlin.
(26) Germar, [E. F.]
1841. maden im kochsalze. Stettin. Ent. Ztg. 2: 126–127.
(27) Goedaert, J.
[1700]. histoire naturelle des insectes selon leurs differentes metamorphoses. 3 t., illus. Middelbourg.
(28) Griffen, E. L., and Back, E. A.
1924. absorption and retention of hydrocyanic acid by fumigated food products. part ii. U. S. Dept. Agr. Bul. 1307, 8 pp.
(29) Grinnan, A. G.
1894. the cheese skipper injuring hams. U. S. Dept. Agr., Div. Ent., Insect Life 6: 266
(30) Harris, T. W.
1841. a report on the insects of massachusetts injurious to vegetation. 459 pp. Cambridge.
(31) Herrick, G. W.
1914. insects injurious to the household and annoying to man. 470 pp., illus. New York.
(32) Howard, L. O.
1896. some insects affecting cheese, hams, fruit, and vinegar. *In* Howard, L. O., and Marlatt, C. L., The Principal Household Insects of the United States. U. S. Dept. Agr., Div. Ent. Bul. (n. s.) 4: 100–111, illus.
(33) ———
1900. a contribution to the study of the insect fauna of human excrement. [with especial reference to the spread of typhoid fever by flies.] Wash. Acad. Sci. Proc. 2: 541–604, illus.
(34) ———
1901. the insect book. 429 pp., illus. New York.

(35) Howard, L. O.
1921. report of the entomologist. [U. S.] Dept. Agr. Ann. Rpt. 1921. 33 pp.
(36) Johnston, W., and Villeneuve, G.
1897. on the medico-legal application of entomology. Montreal Med. Jour. 26: 81–90, illus.
(37) Kellogg, V. L.
1893. insect notes. Kans. Acad. Sci. Trans. (1891/92) 13: 112–115, illus.
(38) Kessler, H. F.
1883. die entwickelungs- und lebensweise der käsefliege, piophila casëi l. (tephritis putris f.). Ber. Ver. Naturk. Cassel 29/30: 58–60.
(39) Kirby, W., and Spence, W.
1822. an introduction to entomology. Ed. 4, vol. 1, illus. London.
(40) Krausse, A. H.
1909. ueber die maden der käsefliege piophila casei l Ztschr. Wiss. Insektenbiol. 5: 394–398, illus.
(41) Linné, C. von.
1758. systema naturae. Ed. 10, t. 1. Holmiæ.
(42) ———
1761. fauna suecica. Ed. 2, 578 pp., illus. Stockholmiæ.
(43) ———
1806. a general system of nature. Translated by W. Turton. vol. 3, pt. 2. London.
(44) Lodge, O. C.
1916. fly investigations reports. iv.—some enquiry into the question of baits and poisons for flies, being a report on the experimental work carried out during 1915 for the zoological society of london. Zool. Soc. London Proc. 1916: 481–518.
(45) Macquart, [P. J. M.]
1835. histoire naturelle des insectes. diptères. t. 2, illus. Paris.
(46) Magnus, O.
1567. historia de gentium septentrionalium variis conditionibus statisubue. Liber 22, cap. 8. Basileae. [Not seen.]
(47) Mégnin, P.
[1894]. la faune des cadavres—application de l'entomologie à la médecine légale. 214 pp., illus. Paris.
(48) Meigen, J. W.
1826. systematische beschreibung der bekannten europäischen zweiflügeligen insekten. Theil 5, illus. Aachen.
(49) Melander, A. L., and Spuler, A.
1917. the dipterous families sepsidae and piophilidae. Wash. Agr. Expt. Sta. Bul. 143, 97 pp., illus.
(50) Merian, M. S.
1730. de europische insecten. 84 pp., illus. Amsterdam.
(51) Mote, D. C.
1914. the cheese skipper (piophila casei linné). Ohio Nat. 14: 309–316, illus.
(52) Motter, M. G.
1898. a contribution to the study of the fauna of the grave. a study of one hundred and fifty disinterments, with some additional experimental observations. Jour. N. Y. Ent. Soc. 6: 201–231.
(53) Murtfeldt, M. E.
1893. the cheese or meat skipper. (piophila casei). U. S. Dept. Agr., Div. Ent., Insect Life 6: 170–175.
(54) Ormerod, E. A.
1900. cheese and bacon fly. piophila casei, linn. *In her* Report of Injurious Insects and Common Farm Pests during the Year 1899 with Methods of Prevention and Remedy (ser. 2, no. 1, 1899) 23: 7–20, illus.
(55) Paterson, A. M.
1919. home preparation of pork. Kans. Agr. Expt. Sta. Circ. 76, 13 pp., illus.

(56) PAVLOSKI, E. N.
1922. [ON THE BIOLOGY OF THE LARVAE OF PIOPHILA CASEI, L., IN CONNECTION WITH THEIR PARASITISM OF MAN.] Separate from Collection of Scientific Works in Honor of the 50-Years Activities in Med.-Sci. of A. A. Netchaeva at the Obukhov Hospital. 7 pp. Petrograd. [Russian original not seen. Reference from Rev. Appl. Ent. (B) 13: 72, 1925.]

(57) PIERCE, W. D.
[1921]. SANITARY ENTOMOLOGY. THE ENTOMOLOGY OF DISEASE, HYGIENE AND SANITATION. 518 pp., illus. Boston.

(58) REDI, F.
1909. EXPERIMENTS ON THE GENERATION OF INSECTS. Translated from the Italian edition of 1688 by M. Bigelow. 160 pp., illus. Chicago.

(59) RILEY, C. V.
1869–70. [NOTE ON THE CHEESE-FLY.] Amer. Ent. 2: 78–79.

(60) ———
1870. CHEESE-FLY AND BLOW-FLY. Amer. Ent. and Bot. 2: 339.

(61) ———
1874. THE RED-LEGGED HAM BEETLE—CORYNETES RUFIPES (FABR.). *In his* Sixth Annual Report on the Noxious, Beneficial, and other Insects, of the State of Missouri, pp. 96–102, illus.

(62) ———
1880. SKIPPERS INJURING SMOKED HAMS. Amer. Ent. (ser. 2, vol. 1) 3: 23–24.

(63) ———
1894. THE INSECTS OCCURRING IN THE FOREIGN EXHIBITS OF THE WORLD'S COLUMBIAN EXPOSITION. U. S. Dept. Agr., Div. Ent., Insect Life 6: 213–227.

(64) RILEY, W. A., and JOHANNSEN, O. A.
1915. HANDBOOK OF MEDICAL ENTOMOLOGY. 348 pp., illus. Ithaca, N. Y.

(65) RONDANI, C.
1874. SPECIES ITALICAE ORDINIS DIPTERORUM (MUSCARIA RNDN.) COLLECTAE ET OBSERVATAE. Bul. Soc. Ent. Ital. 6: 243–274.

(66) RÜHL, M.
1912. ZUR LEBENSWEISE VON PIOPHILA CASEI. Soc. Ent. 27: 15.

(67) SAKHAROV, N. L. (SACHAROW, N. L.)
1921. DIE SCHÄDLINGE DER FISCHPRODUKTE IM ASTRACHAN'SCHEN GOUVERNEMENT. Arb. Biol. Wolga Sta. 6: 1–39. [In Russian. German résumé, pp. 35–39.]

(68) SCHINER, R.
1855. [NOTIZ ÜBER FLIEGEN.] Verhandl. Zool. Bot. Ver. Wien, 5: 37–38.

(69) SCOPOLI, J. A.
1763. ENTOMOLOGIA CARNIOLICA. 420 pp. Vindobonae.

(70) SMITH, J. B.
1896. ECONOMIC ENTOMOLOGY FOR THE FARMER AND FRUIT-GROWER, AND FOR USE AS A TEXT-BOOK IN AGRICULTURAL SCHOOLS AND COLLEGES. 481 pp., illus. Philadelphia.

(71) STEFANI, T. DE.
1915. NOTE DI MYIASIS NEGLI ANIMALI E NELL'UOMO. Rinnovamento Economico-Agrario, Trapani 9: 89–92, 110–113. [Not seen. Reference from Rev. Appl. Ent. (B) 3: 152, 1915.]

(72) SURFACE, H. A.
1913. PESTS OF THE HOUSEHOLD. Pa. Dept. Agr., Div. Zool., Bimo. Zool. Bul. 3: 17–25. illus.

(73) SWAMMERDAM, J.
1758. THE BOOK OF NATURE; OR, THE HISTORY OF INSECTS. PART II. Translated from the Dutch and Latin original edition (1669) by T. Flloyd. Revised by J. Hill. 153 pp., illus. London.

(74) TASCHENBERG, E. L.
1880. DIE ZWEIFLÜGLER, NETZFLÜGLER UND KAUKERFE. 227 pp., illus. Bremen. (*His* Praktische Insekten-Kunde, Theil 4.)

(75) TAYLOR, C.
1861. A CHAPTER ON MITES. Harper's New Mo. Mag. 22: 607–614, illus.

(76) THÉBAULT, V.
1901. HÉMORRHAGIE INTESTINALE ET AFFECTION TYPHOÏDE CAUSÉE PAR DES LARVES DE DIPTÈRE. Arch. Parasitol. 4: 353–361.

(77) UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF ENTOMOLOGY.
1916. IMPORTANT INSECTS WHICH MAY AFFECT THE HEALTH OF MEN OR ANIMALS ENGAGED IN MILITARY OPERATIONS. U. S. Dept. Agr., Off. Sec. Circ. 61, 24 pp., illus.

(78) UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF ANIMAL INDUSTRY.
1921. NOTICES REGARDING MEAT INSPECTION. U. S. Dept. Agr., Bur. Anim. Indus. Serv. and Regulat. Announc. 165: 2–3.

(79) WILDER, F. W.
[1921]. THE MODERN PACKING HOUSE. New ed. rev. by D. I. Davis. 472 pp., illus. Chicago.

(80) WILLARD, X. A.
1869–70. THE CHEESE-FLY. Amer. Ent. 2: 78.

(81) WILLE, J.
1923. BIOLOGISCHE UND PHYSIOLOGISCHE BEOBACHTUNGEN UND VERSUCHE AN DER KÄSEFLIEGENLARVE (PIOPHILA CASEI L.). Zool. Jahrb., Abt. Allg. Zool. u. Physiol. Tiere 39: 301–320, illus.

(82) ZETTERSTEDT, J. W.
1840. INSECTA LAPPONICA. 1139 pp. Lipsiae.

(83) ———
1847. DIPTERA SCANDINAVIÆ. t. 6. Lundæ.

ORGANIZATION OF THE UNITED STATES DEPARTMENT OF AGRICULTURE

January 5, 1927

Secretary of Agriculture	W. M. JARDINE.
Assistant Secretary	R. W. DUNLAP.
Director of Scientific Work	A. F. WOODS.
Director of Regulatory Work	WALTER G. CAMPBELL.
Director of Extension Work	C. W. WARBURTON.
Director of Information	NELSON ANTRIM CRAWFORD.
Director of Personnel and Business Administration	W. W. STOCKBERGER.
Solicitor	R. W. WILLIAMS.
Weather Bureau	CHARLES F. MARVIN, *Chief.*
Bureau of Agricultural Economics	LLOYD S. TENNY, *Chief.*
Bureau of Animal Industry	JOHN R. MOHLER, *Chief.*
Bureau of Plant Industry	WILLIAM A. TAYLOR, *Chief.*
Forest Service	W. B. GREELEY, *Chief.*
Bureau of Chemistry	C. A. BROWNE, *Chief.*
Bureau of Soils	MILTON WHITNEY, *Chief.*
Bureau of Entomology	L. O. HOWARD, *Chief.*
Bureau of Biological Survey	E. W. NELSON, *Chief.*
Bureau of Public Roads	THOMAS H. MACDONALD, *Chief.*
Bureau of Home Economics	LOUISE STANLEY, *Chief.*
Bureau of Dairy Industry	C. W. LARSON, *Chief.*
Office of Experiment Stations	E. W. ALLEN, *Chief.*
Office of Cooperative Extension Work	C. B. SMITH, *Chief.*
Library	CLARIBEL R. BARNETT, *Librarian.*
Federal Horticultural Board	C. L. MARLATT, *Chairman.*
Insecticide and Fungicide Board	J. K. HAYWOOD, *Chairman.*
Packers and Stockyards Administration	JOHN T. CAINE III, *in Charge.*
Grain Futures Administration	J. W. T. DUVEL, *in Charge.*

This bulletin is a contribution from

Bureau of Entomology	L. O. HOWARD, *Chief.*
Stored-Product Insect Investigations	E. A. BACK, *in Charge.*

56

ADDITIONAL COPIES
OF THIS PUBLICATION MAY BE PROCURED FROM
THE SUPERINTENDENT OF DOCUMENTS
GOVERNMENT PRINTING OFFICE
WASHINGTON, D. C.
AT
15 CENTS PER COPY